

CARPOIDS—ECHINODERMS OR CHORDATES?

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CONTENTS

I. Introduction	439
II. The aulacophore theory	441
III. The calcichordate theory	446
(a) Generalities	446
(b) General problems	447
(c) Initial assumptions	448
(1) Mouth and anus	448
(2) The gill slits of cornutes	448
(3) The notochord	451
(4) The nervous system	452
(d) Further problems	454
(1) Calcite and bone	454
(2) The fossil record	455
(e) Insurmountable difficulties	456
(1) The homology of cornutes and mitrates	456
(2) The gill openings of mitrates	457
IV. The organization of carpoids	458
V. The bionomics of carpoids	460
VI. The phylogenetic position of carpoids	462
VII. Summary	466
VIII. Acknowledgements	468
IX. References	469
X. Addendum	471

I. INTRODUCTION

Among Palaeozoic fossils, carpoids are perhaps the most curious and enigmatic. A truly bewildering catalogue of descriptive terms, orientations, interpretations and classifications has been applied to these early echinoderm-like creatures, known generally as the cornute and mitrate carpoids, but now either referred to the echinoderm class Stylophora (Ubaghs, 1968*b*) or the chordate subphylum Calcichordata (Jefferies, 1967 *et seq.*). For the purposes of this review the term 'carpoid' is used to include such animals.

Carpoids are not a large or common group of fossils; in all only some 30 cornute and mitrate genera have been described. They appear first in the early Middle Cambrian with an undescribed cornute genus from Utah (Ubaghs, 1975, p. 85) and with the slightly younger *Ceratocystis* and they are known last from the Lower or Middle

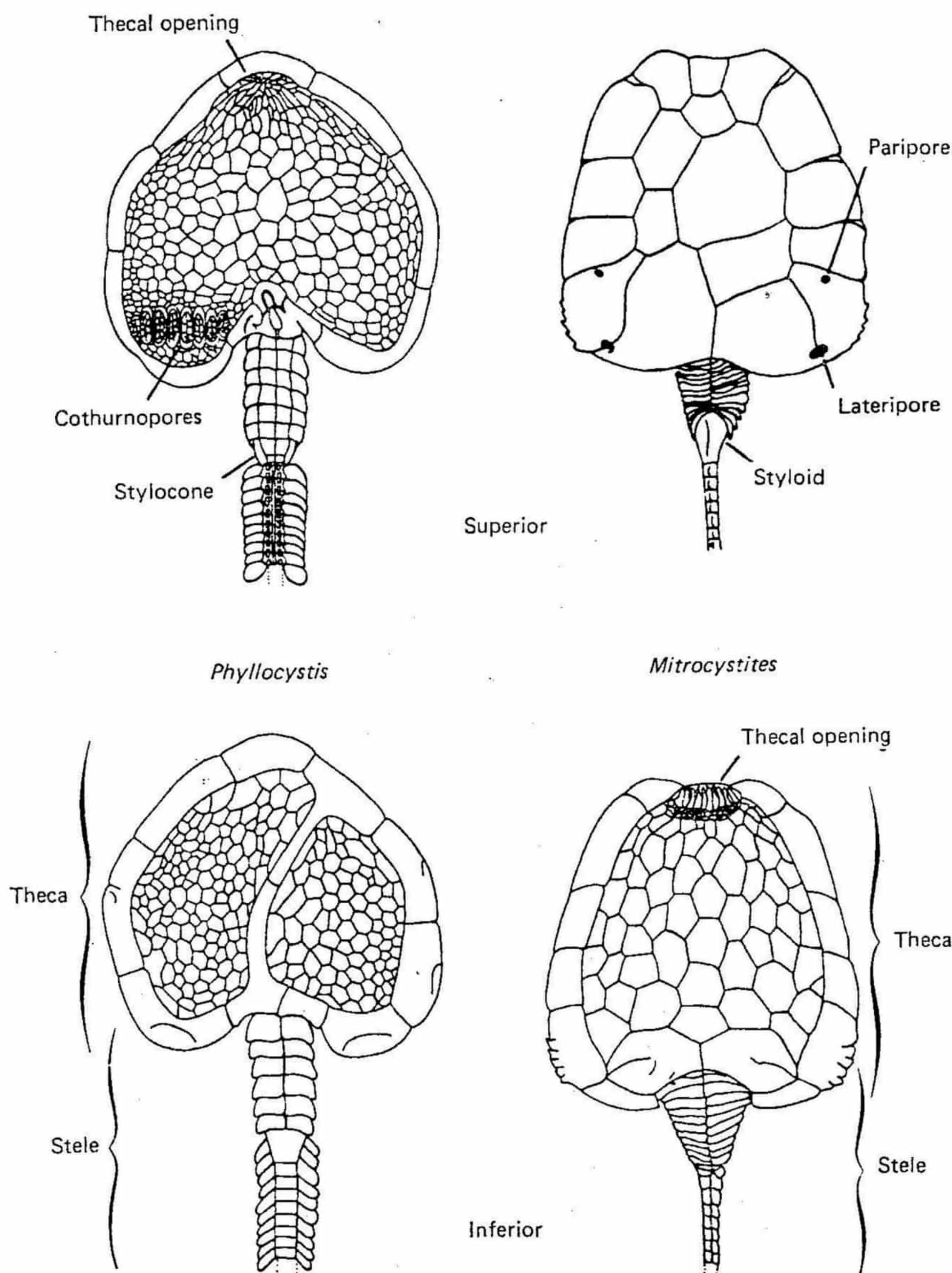


Fig. 1. General morphology of the skeleton of two typical carpoids, the cornute *Phyllocystis* and the mitrate *Mitrocystites*. (After Ubaghs, 1968*b*, fig. 325.)

Devonian. Carpoids have a flattened, polyplacate theca and a tripartite peduncle or stem (referred to here as the stele) (Fig. 1). The skeleton consists of calcite plates with the characteristic reticulate microstructure of echinoderm stereom. The older cornutes are highly asymmetrical with well-differentiated, thickened marginal plates and with the thecal faces covered by smaller scale-like ossicles. The mitrates, which appear first in the Lower Ordovician, tend to be more bilaterally symmetrical, especially the later ones, which also possess a rigid, more box-like theca. Mitrates differ from cornutes

in details of the thecal openings, and in the nature of the middle part of the stele, where an ossicle, the styloid, tends to be flanged and ornate. Fig. 1 shows two typical carpoids – the cornute *Phyllocystis* and the mitrate *Mitrocystites*. A detailed account of the objective morphology of carpoids is given by Ubaghs (1968b).

Traditionally, carpoids have been viewed as asymmetrical pedunculate echinoderms that branched from the pelmatozoan line of descent before the acquisition of pentamerous symmetry. In recent years, however, two deeply conflicting interpretations have been promulgated. Ubaghs (1961, 1963, 1967, 1968b, 1970, 1971, 1975) has viewed the carpoid stele as a food gathering arm – the aulacophore. For Ubaghs, therefore, carpoids represent an aberrant independent branch of the phylum Echinodermata which became extinct without descendants. Jefferies (1967, 1968a, b, 1969, 1973, 1975; Jefferies & Prokop, 1972; Jefferies & Lewis, 1978), in contrast, has seen carpoids as chordates, the stem group from which evolved independently the acraniates, tunicates and vertebrates. With such widely disparate interpretations it is little wonder that there is no measure of agreement at all in the understanding of these animals.

Such a state of affairs, however, is nothing new for carpoids for they have always been the subject of conflicting opinions. The curious skeleton and the variety of thecal openings of the cornutes, in particular, have provided much room for speculation. Fig. 2 shows some of the different morphological interpretations that have been applied to *Cothurnocystis*.

This review of the conflicting ideas, interpretations and speculations must, of necessity, be critical; at the outset it is important to acknowledge the contributions of the several protagonists to the development of the understanding of this curious group of organisms.

II. THE AULACOPHORE THEORY

As mentioned above, Ubaghs (1961 *et seq.*) has interpreted the cornute and mitrate stele as an ambulacral feeding organ which consequently he termed the aulacophore. Now there are other ancient echinoderm groups which possess a similar appendage, particularly the solutan carpoids such as *Dendrocystoides* (Fig. 3). This, however, is regarded by Ubaghs as something separate, in no way homologous with the aulacophore.

In contrast, Caster (1968, 1971) has homologized the solutan stele with that of cornutes and mitrates. The similarity in morphology is striking, as was originally noted by Jaekel (1901, 1918) and Bather (1913). Caster regards the solutan stele as one in which the original primitive feeding function has been lost. The problems inherent in such a view have already been touched upon by Paul (1977). Solute are already armed with a food-gathering brachiole at the other pole of the theca (Fig. 3). Why the fundamental difference in character between the two food-gathering organs? What of the water vascular system? How can a gut be accommodated in such an animal, and what happened to the posterior gut when the aulacophore lost its primitive feeding function? Of the plethora of unlikely interpretations surrounding carpoids, let us first conclude that Caster's is by far the most unlikely. Paul (1977) goes on to

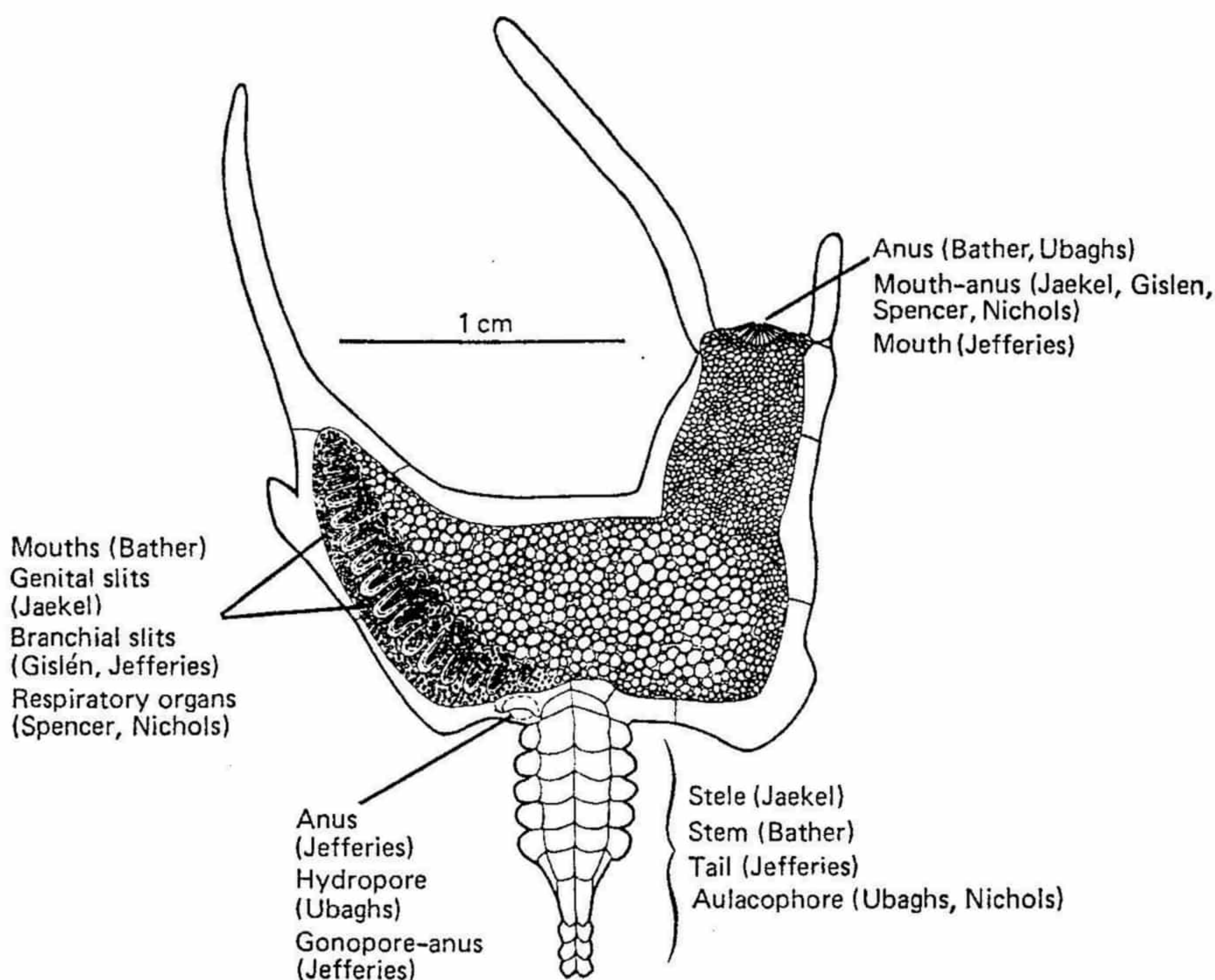


Fig. 2. Interpretations given by various authors of thecal openings, etc. of the cornute *Cothurnocystis*.

agree with Caster that the stele is homologous in all groups, and, therefore, as the solutan stele did not gather food, *ipso facto*, neither did that of cornutes or mitrates.

This, however, slides around the central issue of the aulacophore interpretation. Was it or was it not a food-gathering organ in cornutes and mitrates? The morphology of the stele is well known (Ubaghs, 1968*b*, figs. 343, 344; 1970, figs. 11-14 and Fig. 4 herein). It consists of three parts. Adjoining the theca there is a polyplacate cylinder enclosing a large wide hollow space which communicated with the thecal cavity. This imbricating proximal region is followed by a hemispherical ossicle, in cornutes designated the 'stylocone' and in mitrates the 'styloid'. The distal part of the stele comprises a sequence of symmetrical hemispherical ossicles covered by one or more pairs of small arched plates. Often, in cornutes, these are found folded back to expose the internal surface of the stylocone and that of the hemispherical ossicles of the distal stele. The internal surface is marked by a deep median longitudinal furrow with shallow transverse grooves leading to less obvious lateral depressions (Fig. 4).

Ubaghs interprets these structures as housing an ambulacral food-gathering system, involving a water vascular system. Thus the median groove would contain the (radial?) water vessel, the transverse channels its branches, and the lateral depressions would house the ampullae that served the podia (Fig. 4*e*). Among other echinoderms the analogy is clearly with the ophiuroid arm. As such, the aulacophore theory has some basic difficulties.

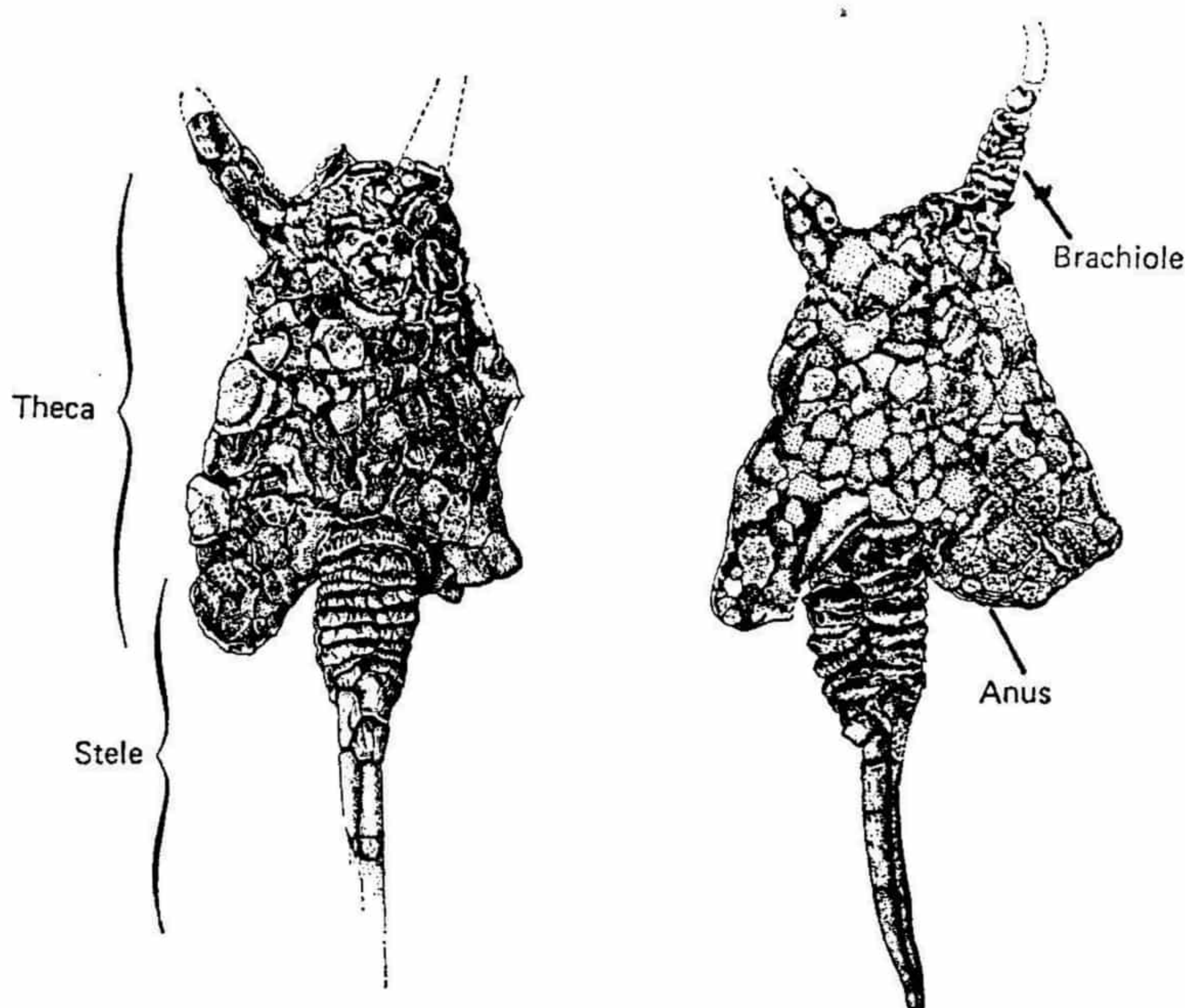


Fig. 3. General morphology of the Ordovician solutan carpoid *Dendrocystoides scoticus* (Bather). Note the similarity between the solutan stele and that of cornutes and mitrates. $\times 1.2$. (After Caster, 1968, fig. 376 and published with permission of the Geological Society of America and the University of Kansas.)

The ophiuroid arm is highly modified from the primitive alternating plates and open ambulacral groove of early sea-stars. Firstly, the podial basins had to become confined to a single ambulacrum (seen first in the genus *Tanaeaster*), then the halves of the so-called vertebrae became opposite and eventually fused (as in the suborder Ophiurina). Thus originated the single fused pieces that occupy the interior of the ophiuroid arm; concomitant with these changes was the transformation of the two inner rows of adaxial ossicles into side plates that hinged and ankylosed to the vertebrae to act as covers. A substantial evolutionary history is therefore implied by such an ambulacral structure and this would seem to prohibit ambulacral structures like this from just appearing without antecedents in the fossil record.

There are other problems. The aulacophore theory requires the presence and persistence of a water vascular system, the external intake of which, the hydropore or madreporite, is readily identified in Palaeozoic echinoderms so equipped. Although Ubags (1968*b*) has identified a thecal opening as a hydropore in some cornutes (the pore that Jefferies (1967, 1968*b*) regards as an anus), the absence of pores in later mitrates, particularly the anomalocystitids, does not permit such an interpretation.

How then can the morphology of the stele be explained? What was the function of the styloid-stylocone, if the stele was primarily a food-gathering organ? One would find the whole interpretation more plausible if the structures interpreted as ambulacral impressions continued into the theca rather than stopping at the stylocone. All interpretations of the stele require a cone of heavy musculature in the proximal stele;

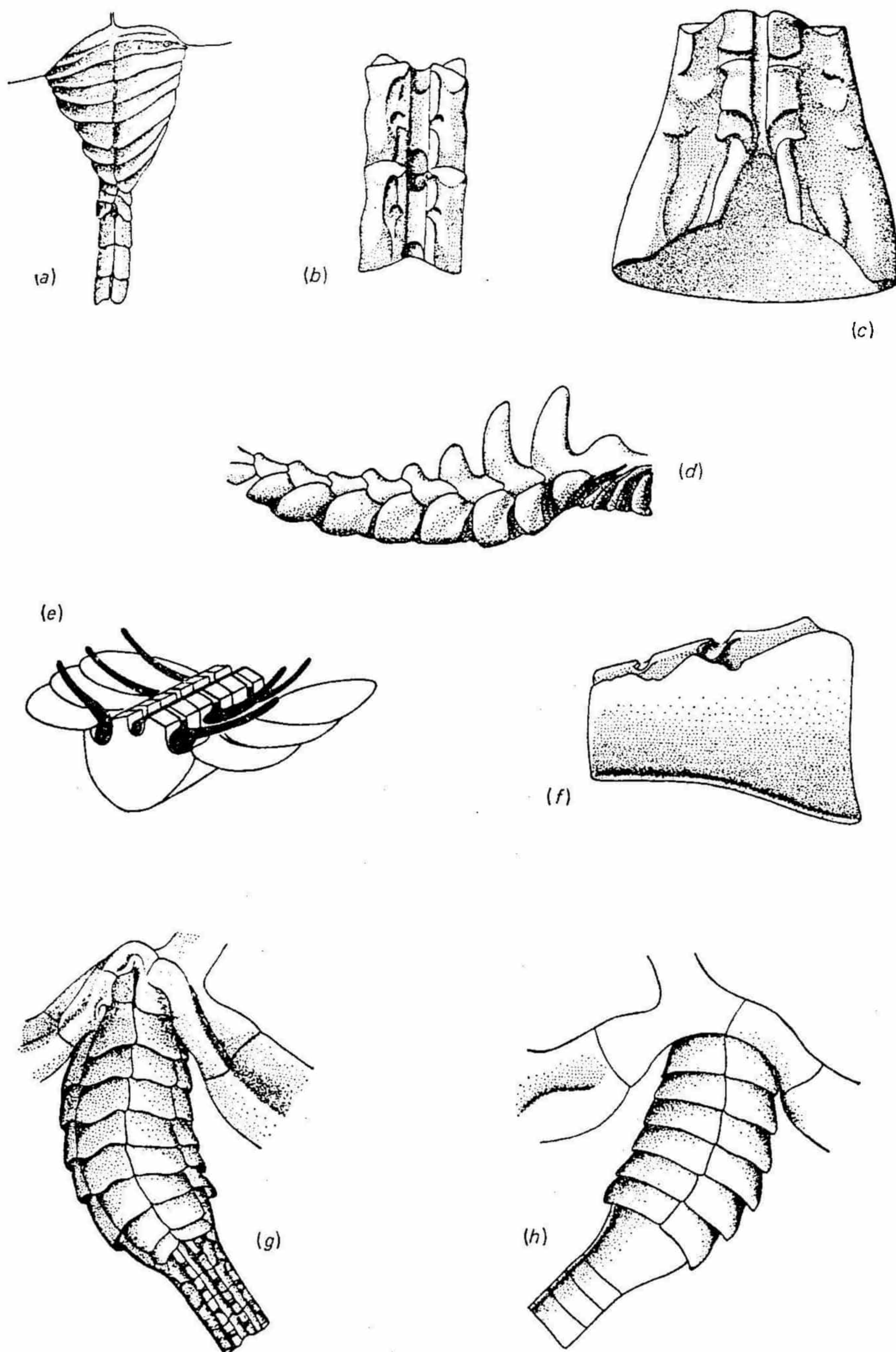


Fig. 4. Morphology of the carpoid stele. (a) Inferior surface of proximal stele of the mitrate *Mitrocystella barrandei* Jaekel. $\times 6$. (After Ubaghs, 1968b, fig. 344.) (b) Interior surface of superior ossicles of the distal stele of the mitrate *Mitrocystites mitra*. $\times 6$. (After Ubaghs, 1968b, fig. 344.) (c) Interior surface of the stylocone of the cornute *Phyllocystis*. $\times 6$. (After Ubaghs, 1968b, fig. 343.) (f) Lateral view of same. $\times 6$. (d) Lateral view of styloid and distal stele of the mitrate *Chinianocarpis thorali*. According to the aulacophore theory the lower plates are the cover plates. Note the occurrence of many intercalary plates which seem to preclude such an interpretation. (After Jefferies & Prokop, 1972, fig. 10.) (e) Interpretation of organization of carpoid stele according to the aulacophore theory. The upper plates are interpreted as cover plates and are shown as being open. The reconstructed podia and water vascular system are shown in black. (After Ubaghs, 1968b, fig. 343.) (g, h) Superior and inferior surface of proximal stele and base of theca of *Phyllocystis*. $\times 5$. (After Ubaghs, 1968b, fig. 343.)



Fig. 5. *Lagynocystis pyramidalis* (Barrande). (a) Posterior face of the theca showing the lack of obvious connexion between stele and theca. $\times 3.2$. (After Ubaghs, 1968b, fig. 341.) (b) Reconstructed median section of the posterior part of the theca and stele. The stippled region is the reconstruction of the brain given by Jefferies (1973, fig. 9).

how did a food groove pass through this? Indeed, in *Phyllocystis* (Ubaghs, 1968b, fig. 340 (1a)) and particularly *Lagynocystis* (Ubaghs, 1968b, fig. 341 (2); Jefferies, 1973, fig. 9) a curtain of calcite skeleton almost seals the interior cavity of the proximal stele from the thecal chamber (Fig. 5). It seems far more reasonable to suppose that the central groove of the stele housed something comparable with a pelmatozoan chambered organ, arising from an aboral nerve centre at the proximal end of the stele, than an ambulacral water vessel and food groove which must enter the theca.

Of course, if the smaller so-called cover plates could not open in life, then this would be fatal to the aulacophore theory. This point has been argued by Jefferies (1968b, p. 291; Jefferies & Prokop, 1972, p. 109; Jefferies & Lewis, 1978, p. 214) for he holds that the stele housed a notochord and so was always enclosed. Whereas in cornutes such as *Ceratocystis* (Jefferies, 1969, pl. 97, fig. 3) and *Phyllocystis* (Ubaghs, 1970, pl. 2, fig. 3a; pl. 5, fig. 2) this remains quite debatable in terms of the morphology of the ossicles concerned, in later mitrates such as *Placocystites forbesianus* (Jefferies & Lewis, 1978) and in an undescribed Australian mitrate, I do not believe that the so-called cover plates could have folded backwards. This situation is well seen in the stele of *Chinianocarpus thoralis* (Jefferies & Prokop, 1972, fig. 10a; Fig. 4d herein). One must agree with Jefferies & Prokop (1972, p. 109) when they write "the way in which the ventral plates imbricate partly inside the dorsal ossicles and partly outside them is not compatible with the view that the plates were adapted to open outwards... It is probably true that an outward opening of the plates is not geometrically impossible in all forms. But from the present standpoint, the forms where opening is impossible are more important than the ones where it is not impossible. The carpoid stele, especially in younger forms, seems to have been an organ of locomotion, rather than of feeding. It had the capacity to enroll so that the plates to the inside of necessity were imbricate and could slip over on another. Hence they were not strongly ankylosed together."

It is here concluded that the stele could not possibly have performed a food-gathering function in all carpoids and so the aulacophore theory is rejected. The notochordal interpretation is discussed in Section III, c 3 and the likely origin and homologies of the carpoid stele are reviewed in Sections IV and VI.

An even more fantastic interpretation of the carpoid stele has been given. Presumably, on the assumption that it is a food-gathering organ, on the observations that the so-interpreted 'cover plates' could not open and that the distal end of the stele is

always missing (cf. Jefferies & Lewis, 1978, p. 244, "neither we, nor anyone else so far as we know, has ever seen an untruncated end to the tail"), the stele has been viewed as a sort of feeding tube, used for sucking up mud in the manner of a vacuum cleaner (Haude, 1978).

However, the well-preserved material of the undescribed Australian mitrate, alluded to above (p. 445), clearly shows the distal termination of the stele.

III. THE CALCICHORDATE THEORY

(a) *Generalities*

The close biological affinity of chordates and echinoderms has long been promulgated. Both groups are tricoelomate, deuterostomatous with similar larvae, radial cleavage and representatives of both groups have a pulsatile pericardial vessel (Booolootian & Campbell, 1964). There are similarities in the detailed structure of the nervous system, the mesodermal skeleton and even in the biochemistry (Bone, 1972).

Gislén (1930) was the first to discuss at length the comparisons that can be made between carpoids and living lower chordates, amphioxus in particular. He was careful to point out, however, that (p. 201) "it has not been my intention to assume the latter to be actual ancestors of the former" (*pace* Jefferies, e.g. 1968*b*, p. 164). Other workers have been impressed by the similarities between carpoids and early vertebrates. For example, Gregory (1936, 1946) speculates that "the stalk is well jointed and might have been translated into a vibratile tail and notochord". So he found carpoids providing "a real if remote relationship between echinoderms and chordates". Other authors have commented on the comparison between the ornament and microstructure of skeletal elements of carpoids and ostracoderms (Caster, 1952; Caster & Eaton, 1956).

These early comparisons of carpoids with chordates have been developed and extended by Jefferies (1967, 1968*a, b*, 1969, 1973, 1975; Jefferies & Prokop, 1972; Jefferies & Lewis, 1978) who has sought to explain the wealth of structure of carpoids in terms of chordate morphology. Carpoids originally (Jefferies, 1967) were set apart in the subphylum Calcichordata (phylum Chordata), being held as ancestral to all chordates – the acraniates, the tunicates and the vertebrates. As the group is thus paraphyletic in a Hennigian sense, it is now recommended that the term calcichordata be used only informally (Jefferies & Lewis, 1978).

In bare outline the calcichordate theory may be summarized thus. The thecal openings on the left side of *Cothurnocystis* and other cornutes are seen as functional gill slits (cf. the development of amphioxus in which the gill slits appear first on the left-hand side). The major thecal opening of cornutes is interpreted as a mouth and a pore opening near the stele is seen as an anal opening (in some cornutes, e.g. *Scotiaecystis*, this is internal). The theca of typical cornutes is reconstructed with four (later, in 1975, five) chambers designated the buccal cavity, the left pharynx, the anterior and posterior coeloms (left and right anterior coeloms in 1975). In mitrates such as *Mitrocystites* right gill slits are also developed and so is a corresponding right pharynx. Also inferred are internal gill slits that open into left and right atria, and a rectum that opens into the left atrium (cf. a tunicate tadpole). Mitrates therefore have paired gill

openings with the faeces leaving the theca through the left gill opening. The carpoid stele is interpreted as containing a notochord with a dorsal nerve cord, together with muscle blocks. The various canals running within and along the internal surface of the theca are seen as nerves, which, after reconstruction, are found to lead to an enlarged ganglion at the base of the theca, designated the brain. This is reconstructed in detail, for example, in *Mitrocystella*, and is found to be morphologically similar to that of *Petromyzon* or of a cephalaspid, except for being shorter. As evidence for its fish-like character homologues of the trigeminal complex and trigemino-profundus ganglia of the olfactory, optic and lateralis complexes are all recognized. A small slit in *Mitrocystites* is interpreted as a lateral line; paired pores toward the posterior of the theca of *M. mitra* are held to house eyes; in fact two types of eyes are identified, namely transpharyngeal and cispharyngeal; the latter are homologues of vertebrate eyes. A ventral atrium is seen in the mitrate *Lagynocystis pyramidalis*. This form is considered to give rise directly to amphioxus and the cephalochordates (with the loss of calcite skeleton, the loss of a fish-like brain and other changes). Another mitrate group, close to *Peltocystis* and its allies, with an independent loss of skeleton, gave rise to tunicates. A further mitrate group took to continuous swimming, lost its calcite skeleton, acquired a phosphatic one and gave rise to vertebrates.

This series of propositions, welded now into a coherent theory through some 500 pages of interpretative writing published among some of the more prestigious British journals, has already suffered serious criticism (Denison, 1971). Nevertheless, the theory is finding at least some acceptance (e.g. Eaton, 1970; Bone, 1972; Paul, 1977, p. 124). Ubaghs (1975) justifiably complains that it is based largely on reconstructed soft parts. Yet it should be possible to identify the theory's basic assumptions, to examine its broader implications and test its validity. What follows is an attempt to do just this.

(b) General problems

A number of critical comments of a general nature have already been published in discussion of Jefferies's original paper. Raised there (Jefferies, 1967, pp. 203–208) are problems that might be termed both conceptual and topographical. For many biologists it must be difficult to envisage a craniate ancestor in which the whole of the alimentary system is anterior to the notochord with the brain squashed up at the hind end of the animal. Also, if the animals possessed functional gills, where are the gill arches? Jefferies (1967) originally and correctly emphasized that his interpretations are incompatible with the view that the vertebrate head was fundamentally segmented. He first identified the carpoid theca with the vertebrate head and body, but more recently Jefferies & Lewis (1978) have homologized it with the head alone, suggesting that the vertebrate trunk developed later. This would appear to remove some of the topographical problems. However, others remain. It is difficult for example to imagine an animal seven-eighths of the body of which is pharynx. An enormous plasticity is attributed to these animals in their evolution. Thus, for example, in deriving amphioxus directly from *Lagynocystis*, Jefferies (1973, pp. 461–462) notes five similarities (including the asymmetry of the inferred anus and suggested rotation during swimming) whereas he invokes seven major changes in the fundamental organization

of the animal, which in combination most biologists would consider as providing good reason for *Lagynocystis* having nothing at all to do with amphioxus. The calcichordate theory abounds with similar matters of emphasis.

(c) *Initial assumptions*

(1) *Mouth and anus*

The calcichordate theory makes some initial assumptions as to the thecal openings in cornutes. As indicated above, there has been no particular agreement as to what these openings were, for example, in *Cothurnocystis*, the best-known and most discussed cornute (Fig. 2). In fact, Jefferies and his co-workers are alone in interpreting the distal opening as a mouth and the small pore at the base of the theca as the anus. In general the anal opening of thecate Palaeozoic echinoderms is distinguished from the other openings by a valvular pyramid of plates, that was presumably closed in life by a sphincter muscle (e.g. edrioasteroids, ophiocystioids, cystoids, eocrinoids, solutan carpoids, crinoids, etc.). The distal orifice of cornutes is different from others, as observed by Ubaghs (1968*b*, p. S513), who judged the surrounding integument to have been very flexible and extensible, "suggesting that the anal orifice could have been protruded and retracted". Spencer (1938) interpreted this integument as closing the entrance of a vestibule that housed the mouth and anus (Section V). The pore identified by Jefferies as the anus is unlike that of any other echinoderm not only in lacking any valvular plates but also in its small size (Fig. 1). Ubaghs (1968*b*) homologizes this pore in cornutes with a similarly placed small slit in *Mitrocystites*, which, however, is interpreted by Jefferies as a lateral line. Objective morphological evidence indicates that the pore in cornutes is more likely to be either a goniopore or a hydropore than an anus. Indeed, its small size (less than a quarter of a millimetre in diameter) and the fact that it passes through solid calcite skeleton (in *Ceratocystis* and *Scotiaecystis*; Jefferies, 1967, fig. 6) would seem to rule out the possibility that it contained a rectum. In mitrates such a problem does not arise, for the anus is inferred as being internal and further inferred as opening into a left atrium.

(2) *The gill slits of cornutes*

The upper surface of the theca of cornutes has a number of thecal openings confined to the bottom left-hand corner ('sutural pores', 'cothurnopores' and 'lamellipores' of Ubaghs, 1968*b*). These vary widely in number and detailed structure. They are well described both by Jefferies (1968*b*) and Ubaghs (1968*b*, pp. S518-521, figs. 336-338; 1970, pp. 26-28) although these authors disagree in minor details. The variation in structures involved is depicted in Fig. 6.

The pores may be simple holes that vary from being located linearly along sutures (as in *Ceratocystis*) to a cluster of pores (as in *Reticulocarpos*). In *Cothurnocystis* and *Phyllocystis* they are complex structures covered by a flap, which, according to Jefferies, acted as an outlet valve. Ubaghs (1968*b*) notes that they vary in number according to size and species. Particularly noteworthy are the so-called lamellipores of *Scotiaecystis*. These consist of narrow slits between vertical calcareous lamellae. They are very numerous (up to about 50), closely set and grouped to form elongate lozenge-

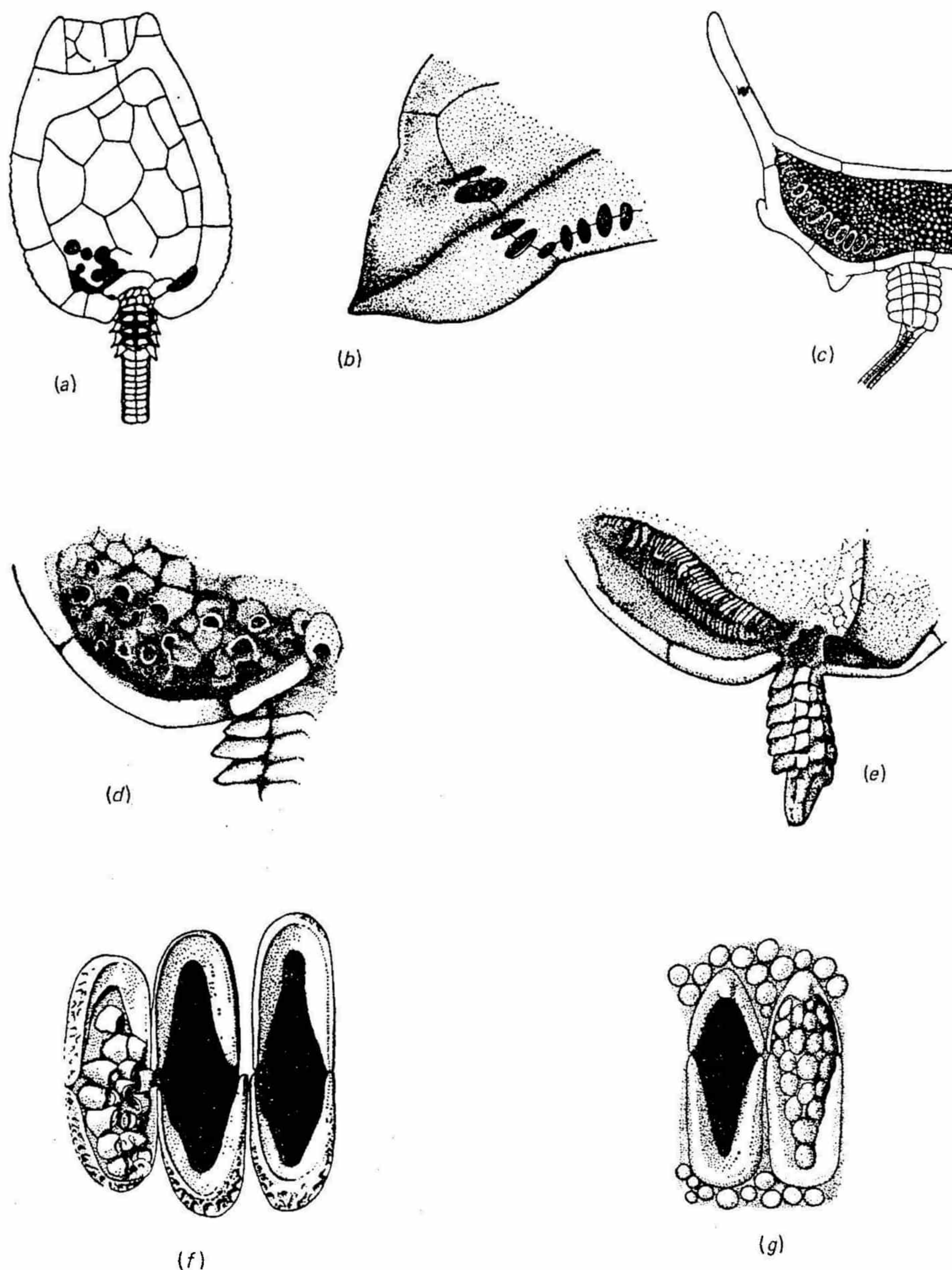


Fig. 6. Thecal pores and slits of the left corner of the theca of various cornute carpoids indentified as gill-slits according to the calcichordate theory. (a) *Reticulocarpos hanusi*. The larger pores at the bottom left and right of the theca are described as the left and right optic embayments by Jefferies & Prokop (1972). (After Jefferies & Prokop 1972, fig. 3.) (b) Sutural pores of *Ceratocystis perneri* Jaekel. $\times 3$. Jefferies (1969) distinguishes accessory gaps from gill-slits of which he identifies seven. (After Ubaghs, 1968b, fig. 336.) (c) Cothurnopores of *Cothurnocystis* extending deeply into the spinal corner of the theca. (After Ubaghs, 1968b, fig. 346.) $\times 1$. (d) Thecal pores of *Phyllocystis crassimarginata* Thoral. $\times 6$. (After Ubaghs, 1970, pl. 4, fig. 2.) (e) Lamellipores of *Bohemiaecystis bouceki* Caster. (After Ubaghs 1968b, fig. 338.) $\times 2$. (f, g) Different detailed structure of the cothurnopores of *Cothurnocystis* given by Ubaghs (1968b, fig. 336) and Jefferies (1968, fig. 2). $\times 12$ approx.

shaped structures similar to the conjunct pore-rhombs of some cystoids. All-in-all they form a curious and varied array of pores and related structures.

For Jefferies these structures constituted the gill slits of cornutes and so connected directly with the pharynx in the inside of the theca. In *Ceratocystis*, the oldest described cornute, Jefferies (1969) interprets seven of the thecal pores as gill slits and concludes (p. 532) "that this was probably the primitive number for cornutes and therefore chordates in general". The interpretation of these pores as gill slits is another initial keystone of the calcichordate theory.

Ubaghs (1968*b*, p. S524) judiciously sums up the matter. Concerning the accessory pores he states "their complex morphology and their narrow location in a definite part of the body suggest that they housed specialized structures or were connected with internal organs such as the alimentary canal. This leads to consideration of the possibility that they were branching openings related to the pharyngeal part of the digestive tract... The accessory pores... could not have been gill slits opening directly to the exterior, for cothurnopores in many specimens of *Cothurnocystis elizae* penetrate so deeply into the spinal corner of the theca that the digestive tube would have bent to an acute angle at the end of the branchial region, which is unlikely. Therefore, if they were connected with the alimentary canal, they could have been external openings of branchial sacs or diverticles. But in such case why did they require the complex plated structure of cothurnopores, why were they so different from one genus to another and even from one species to another species of the same genus, and how is it possible that they are entirely lacking in some species?"

With Ubaghs and with Denison (1971, p. 1134) one must conclude that it is unlikely that these pores served as gill slits.

What then was their function? There is a strong analogy with the various respiratory modifications of contemporaneous Palaeozoic echinoderms (such as the epispires of eocrinids, the diplopores, pectinirhombs and goniospires of cystoids) and it seems most likely that this was their purpose. Nichols (1962) has suggested that the covered pores of *Cothurnocystis* housed respiratory organs that could be retracted when the animal was disturbed. This, perhaps, is as good an explanation as any.

One of the more notable aspects of fossil echinoderms is the wide variety of specialized respiratory organs developed in the Lower Palaeozoic. Paul (1977, pp. 147-148), in reviewing these, poses the question "Why did endothelial pore structures become extinct at the close of the Palaeozoic when they appear to be highly efficient?" Perhaps this was related to the oxygen concentration of sea water. Some writers correlate the build-up of atmospheric oxygen with the evolution of life (Berkner & Marshall, 1965). They see the relatively sudden appearance of diverse life at the base of the Cambrian as the time when atmospheric oxygen had built up to a level at 1% of that of the present day. Low oxygen concentration in the seas would provide a respiratory requirement for early Palaeozoic echinoderms not encountered by their descendants. However, some other writers maintain that the level of atmospheric oxygen of the Precambrian was similar to that of to-day (Dimroth & Kimberley, 1976).

It is of interest to note that Jefferies & Lewis (1978), in their harmonizing of the 'segmentationist' and 'antisectionist' view of the origin of vertebrates, identify

vertebrate somites in mitrates and cornutes. They homologize, *inter alia*, the hyoidean somite and the first calcichordate tail segment! Now it is generally agreed that the hyoid gill slit is the most anterior one and then it appears only in some fossil agnathans and larval lampreys. For the carpoid 'gills' to have anything to do with those of vertebrates they would have been obliged to move off the theca and down the stele.

(3) *The notochord*

The morphology of the carpoid stele has been discussed in some detail in Section II. The distal part of the stele consists of a series of hemispherical ossicles covered over by arched plates. The surface of the ossicles is marked by a longitudinal furrow with shallow grooves leading to less obvious lateral depressions. Ubaghs has interpreted the stele as a food-gathering organ which accommodated a water vessel and podia. For Jefferies it housed a notochord. His original interpretation of the stele of *Cothurnocystis* is as follows (1967, pp. 171–172): "The median groove of *C. elizae* probably contained the chambered organ or notochord, coated at least partially with the peduncular nerve or dorsal nerve cord... The imbricated dorsal plates suggest that the stem could flex upwards requiring muscles. These were probably seated in the lateral grooves and divided into blocks. Such blocks... probably straddled the sutures between successive ventral ossicles. Muscles would require nerve and blood supply, and the transverse grooves may represent lateral vessels connecting the muscles with a peduncular vessel running down the middle of the chambered organ. By analogy with mitrates, lateral nerves, with ganglia probably emerged dorsal to each lateral blood vessel."

From this description it can be seen that Jefferies (1967, p. 170; 1969, p. 524) originally homologized the crinoid stem and the chordate notochord. Subsequently (1975, pp. 254–255) he has modified this view, still maintaining the homology of the carpoid stele and the vertebrate tail, but holding that the stem of stemmed echinoderms is but a parallel structure. He writes (1975, p. 255): "There is functional-morphological evidence that the tail of calcichordates contained a notochord. The conclusion, therefore, that stems and tails are parallels rather than homologues does not greatly alter the arguments for connecting calcichordates with other chordates, which are now confirmed by detailed resemblances of their pharyngeal structures with those of tunicates."

There now arises a central morphological problem of the calcichordate theory. cursory examination of Jefferies's work reveals that his inferred notochord and dorsal nerve cord is borne *dorsal* to the hemispherical ossicles in cornutes and *ventral* in mitrates. This interpretation is forced by the identification of thecal faces, which, in turn, stems from the supposed homology of the reconstructed thecal chambers – the centre piece of the calcichordate theory.

For Jefferies the proximal stele of cornutes alone is homologous with the complete stele of mitrates, the stylocone and distal stele (with the 'notochord') having "dropped off". This process is seen as taking place in the reduced distal stele of the late cornute *Reticulocarpos*. Mitrates then grew another stylocone (styloid) and distal stele, this time with the solid calcite rings *above* the notochord. One must sympathize with

Ubaghs (1975, p. 87) who finds all this "difficult to believe". For it is almost impossible to envisage animals undergoing such radical morphological changes. Could the carpoid stele have housed a notochord? There is no compelling evidence that it did and it is conceptually difficult to see how it would have been possible. The inferred myotomes (muscle blocks) would not seem to have been able to function, enclosed as they were by calcite ossicles. There could have been no scope for the serial contraction and undulatory movement, in response to which a notochord presumably developed. The stele plates containing the so-called notochord cannot be compared with the dermal elements of vertebrates for these never immediately enclose the notochord. Denison (1971, p. 1134) exclaims "Surely there can be no serious thought of comparing them with vertebrae, which were absent in primitive vertebrates." Yet this seems to be the intention (Jefferies & Lewis, 1978, pp. 310-312).

There is no good reason to infer that the carpoid stele housed anything comparable with a vertebrate notochord. However, it seems to have contained strong musculature and perhaps an extension of an aboral nerve centre similar to the pelmatozoan chambered organ (Section IV). In later forms it may well have been an organ of locomotion.

(4) *The nervous system*

The calcichordate theory involves the interpretation that the animals possessed a fish-like nervous system. Various channels, seen particularly on the inside of the thecal plates of mitrates, are interpreted as nerves leading to an enlarged ganglion, the brain, at the base of the theca (e.g. *Mitrocystites mitra*; Fig. 7a). The extent of reconstruction can also be seen in Fig. 7(b) in which the objective channels and impressions alone are included. In *Mitrocystella incipiens miloni*, to be sure, internal casts indicate more of these internal grooves, and especially their confluence toward the base of the theca (Jefferies, 1968b, pl. 5, fig. 11). But, even allowing the validity of the reconstruction, one can only be impressed by the differences in detail between the nervous systems of *M. mitra* and *M. i. miloni* (cf. Jefferies, 1968b, fig. 19 and 27).

This lack of persistence in the nervous system is striking. The 'brain' of the cornute *Ceratocystis* is constructed with "a dorsal process" that "would represent a sort of primitive median eye". "This however was not homologous with pineal or parapineal eyes of vertebrates, since it was absent in the group of cornutes...from which mitrates and therefore all modern chordates descended" (Jefferies, 1975, p. 270).

A small groove on the underside of *Mitrocystites* is interpreted as the beginning of a lateral line system. The anterior pair of pores in the upper surface are interpreted as "transpharyngeal" eyes while the posterior ones were thought to be sensory areas for touch (Jefferies, 1975, p. 282). In the closely related *Mitrocystella*, the eyes are vestigial. Now external eyes and a lateral line system would seem to be eminently sensible developments for organisms experimenting with a motile mode of existence. Yet in later mitrates they are absent.

I agree with Chauvel (1941) and Jefferies that the channels that traverse the inside of the carpoid theca are best interpreted as the paths of nerves. However, unlike the vertebrate cephalic nervous system, they show enormous variation and plasticity. It is

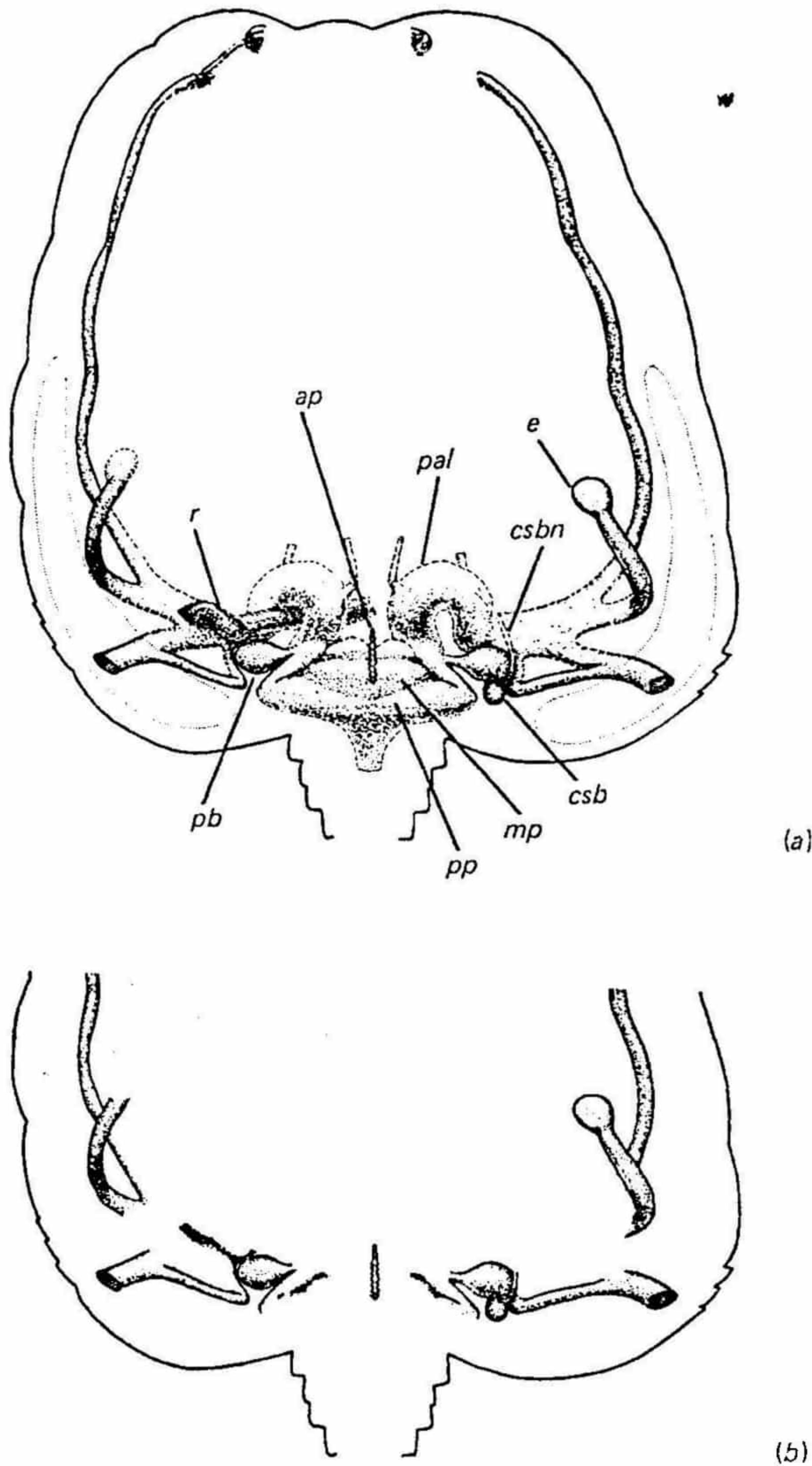


Fig. 7. (a) Reconstruction of the dorsal aspect of the brain and cranial nerves of *Mitrocystites mitra* given by Jefferies (1968*b*). *ap*, Anterior part of brain; *csbn*, nerve to carrot-shaped body (nerve to lateral line ganglion); *csb*, carrot-shaped body (lateral line ganglion); *e*, eye; *mp*, median part nerves; *pal*, palmar nerve; *pb*, pyriform body; *pp*, posterior part of brain; *r*, rectum. (After Jefferies, 1968*b*, fig. 27, q.v. for greater detail.) (b) The same impressions on which the reconstruction is based.

possible to see some similarity in the pattern of lateral branching of the canals and the cranial nerves of vertebrates but details of their identification are highly speculative (cf. Tarlo, in Jefferies, 1968*a*). What seems impossible in carpoids, however, is the presence of an enlarged central ganglion that could be construed as a brain. This inferred brain is shown in reconstructions (e.g. Jefferies, 1973, fig. 8, 9; Jefferies & Lewis, 1978, fig. 25) as filling the entire proximal stele cavity, covering what Ubaghs

(1968) termed the aulacophore apophyses (cf. Fig. 5). I would prefer to interpret these apophyses as places of insertion of muscles attached to the imbricating plates of the proximal stele and to the stylocone. Hence there would have been little space at all available for any enlarged nerve ganglion.

The fact that the so-interpreted nerve canals traverse the inside of the endodermal skeleton is, of course, not reminiscent of chordates but is seen for example in crinoids (e.g. Philip, 1961, p. 149; Denison, 1971). The channels that radiate from near the base of the theca suggest the presence of an aboral nerve centre at the base of the theca similar to that of pelmatozoans.

(d) *Further problems*

(1) *Calcite and bone*

In viewing carpoids as stem vertebrates, ancestral to tunicates, acraniates and vertebrates, it is necessary to postulate that the carpoid endoskeleton was lost independently in three lines of descent; in the line that led to fishes the calcite skeleton was replaced by bone. There is no known way in which this could be done directly for the echinoderm calcite originates intracellularly, while vertebrate apatite is seeded extracellularly by the collagen fibres (Sognnaes, 1960). Eaton (1970, p. 975), however, does suggest the direct replacement of calcite by bone, but clearly there are great difficulties.

The endoskeleton of thecate echinoderms is, of course, a most important feature of the architecture of the animal. Imagine an echinoid or a crinoid trying to function without its skeleton! Jefferies recognizes this problem, for the skeleton was lost "producing a cartilagenous skeleton like that of some holothurians. Later the collagen in the cartilage began to seed apatite in a vertebrate fashion" (1967, p. 201).

This is contrary to an accepted view on cartilage and bone. Romer (1942) has argued that cartilage is an embryonic specialization. Halstead (1969, p. 44) observes "As far as evolution is concerned there is no evidence whatsoever to suggest any direct connection between cartilage and bone. Bone evolved as a dermal structure, in all likelihood as a chemical store, but later became protective in function, whereas cartilage was probably an internal supporting function to be eventually replaced by bone."

Hill (in Jefferies, 1968*a*) points out that evidence from at least three fields of study suggests that, among organisms, evolution is generally from phosphate to calcite rather than the reverse. Jefferies's allusion to the skeleton of holothuria is difficult to understand. These echinoderms have a leathery dermis that constitutes the greater part of the body wall. This is composed of connective tissue fibres forming a mesh that encloses the endoskeletal ossicles. The dermis is followed by a layer of circular muscle fibres that may form a complete cylinder. I know of no material comparable with vertebrate cartilage occurring in holothuria, or for that matter in any echinoderms (cf. Person & Philpot, 1969). Therefore, not only is it unlikely that the echinoderm endoskeleton was lost in three independent lines of descent, but also it is difficult to conceive how this could be brought about in a world of real organisms.

Jefferies & Lewis (1978) interpret irregularities in the internal surface of the theca

of *Placocystites forbesianus* as indicating resorption and they further state (p. 213) that "In members of all three stem groups... there are signs of resorption of the skeleton in the adult."

Exactly the opposite is shown by the evolution of the fossils. In early cornutes the thecal faces are covered with thin scale-like ossicles embedded in an integument. In the Upper Cambrian cothurnocystid *Nevadaecystis americana* the upper face is covered by stellate ossicles separated by uncalcified areas (Ubaghs, 1963). In the early mitrates the lower surface retains its scale-like appearance, but the upper surface had become rigid. This trend is continued into the anomalocystitids, the last of the carpoids, where the theca is box-like and both surfaces may be covered with rigid, strongly ankylosed plates (as in *Placocystites*).

(2) The fossil record

The calcichordate literature draws heavily on the concepts of Hennig (1966) in reconstructing phylogenetic relationships (e.g. Jefferies & Lewis, 1978, pp. 207–209). It is not doubted that such approaches are of value in developing schemes of animal relationships; however, conjectured phylogenies must consider geological occurrences (see, for example, Philip, 1965). Palaeontologists unfamiliar with Hennigian concepts may be surprised to see the mid-Silurian carpoid *Placocystites* described as a 'stem vertebrate'.

The calcichordate theory has mitrates as the central group. *Lagynocystis*, from the Middle Ordovician of Bohemia, is said to give rise directly to amphioxus and the acraniates. The Lower Ordovician *Peltocystis* and its allies are claimed to be ancestors of tunicates. Vertebrates are derived from the mitrocystitids and anomalocystitids; the mitrocystitids appear first in the Lower Ordovician, but it is not until the Middle Ordovician that *Mitrocystites* occurs. It seems that mitrates evolved from cornutes in the Lower Ordovician through such a form as *Reticulocarpos* (Jefferies & Prokop, 1972).

The knowledge of the oldest vertebrates in the fossil record has been extended in recent times. Bockelie & Fortey (1976) described the ostracoderm *Anatolepis heintzi* from the Lower Ordovician of Spitzbergen. More recently Ritchie & Gilbert-Tomlinson (1977) have described a late Arenigian or early Llanvirnian fauna from central Australia. This fauna is notable because of the diversity of agnathans present which implies a longer evolutionary history for the group than was previously suspected. This was confirmed by Repetski (1978) who has identified *Anatolepis* from the Late Cambrian Deadwood Formation of Wyoming and recorded bony fragments from rocks of similar age in Alaska, Greenland and Spitzbergen. The fossil record suggests that mitrate carpoids could not have given rise to vertebrates.

Durham (1971) has reviewed knowledge of the origin of deuterostomes as shown by the fossil record. He concludes: "If the enigmatic Early Cambrian *Emmonsaspis* is a cephalochordate and the Middle Cambrian *Eldonia* is tunicate instead of holothurian, it appears probably that the separation of the acraniates and the vertebrates may have occurred in the Precambrian." This view is reinforced by the fossil *Pikaia gracilens* Walcott from the Middle Cambrian Burgess Shale. Although originally regarded as

a worm, Conway Morris (1977) has recently suggested that it is a primitive chordate, with a longitudinal bar comparable to a notochord. Examination of the material (by courtesy of Dr Conway Morris) shows it to be an animal very close to amphioxus. It seems unlikely that a mid-Ordovician fossil could be ancestral to a mid-Cambrian one. Indeed, the fossil record provides strong evidence that the mitrate carpoids could not have given rise to any chordate group.

(e) *Insurmountable difficulties*

(1) *The homology of cornutes and mitrates*

As indicated above (Section III, c 2) there is difference of opinion as to which thecal face of a mitrate is equivalent to which in a cornute.

Jefferies (1973, p. 420) puts his view thus:

An alternative interpretation of the homologies of mitrates and *Reticulocarpis* [a late cornute] is also possible, in many ways opposite to the one adopted here. According to this alternative interpretation the flat ventral surface of mitrates, which I consider dorsal, would be homologous to the flat surface of *Reticulocarpis*, which I consider ventral. Consequently the strut would be homologous to the oblique ridge; the ossicles of the hind stem would be homologous in both mitrates and cornutes; the spikes of the stem ossicles of *Reticulocarpis* would be homologous with the blades on the stem ossicles of mitrates; the stylocone of cornutes would be homologous to the styloid of mitrates; and the paired plates of the mid- and hind-stem would be homologous in cornutes and mitrates.

The arguments against this alternative interpretation rest on the basic asymmetries of the chambers inside the cornute and mitrate thecas, with the primary pharynx anterior to and left of the anterior coelom. This basic arrangement is still discernible in mitrates though greatly modified by the appearance for the first time of the right pharynx which lifted the anterior coelom up from the floor of the theca, squashed it against the ceiling and pushed it in a median direction.

For Jefferies a mitrocystid resembled "a giant calcite-plated tunicate tadpole. It had in common with the latter, buccal cavity, pharynx, internal gill slits, paired atria and gill openings, a rectum that opened into the left atrium..." (Jefferies, 1967, p. 199). In order to produce this animal it is necessary to get from left-sided cornutes (cf. the first appearance of gill slits on the left side of larval amphioxus) to animals with a left and right pharynx and paired gills. To do this Jefferies's homology of thecal faces must be followed (Fig. 8).

Such an identification, demanded by the calcichordate reconstruction, leads to all sorts of problems with the stele. As indicated above, it is necessary to postulate that the proximal stele of the cornute alone is homologous with the mitrate stele. The stylocone and distal stele (and 'notochord') of cornutes "drops-off" and is replaced in mitrates by the styloid and distal stele, an incredible requirement.

For Jefferies (1975, p. 283) the first mitrate was the "first chordate with right gills and right pharynx... a 'hopeful monster' and the child of cornute parents". He finds no problem in the fact that the gill openings are now underneath the animal against the sea-floor for "the analogy of modern rays and skates shows that they could have functioned in this position" (Jefferies, 1968, p. 282). That he interprets later mitrates as living almost entirely buried in mud is not mentioned. What he also does not point

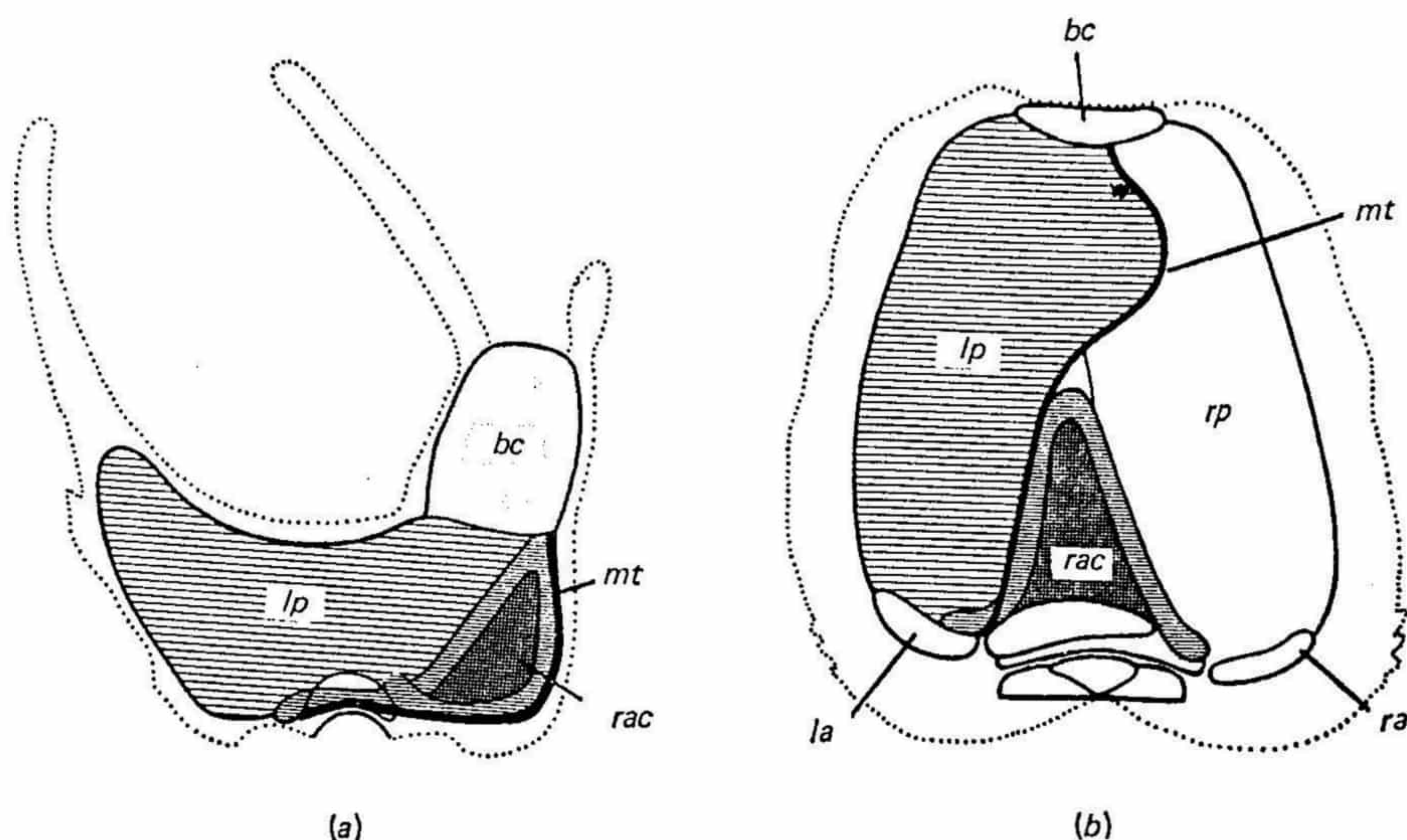


Fig. 8. The interpreted body chambers of the cornute and mitrate carpoids according to the calcichordate theory. (a) The cornute *Cothurnocystis*. (b) The mitrate *Mitrocystites*. *bc*, buccal cavity; *lp*, left pharynx; *rac*, right anterior coelom; *mt*, mesenteric trace. The mitrate condition is derived by development of a right pharynx (*rp*) which lifts up the right anterior coelom and squashes it against the roof of the theca. Right (*ra*) and left (*la*) atria are then developed. For simplicity the purely virtual left anterior coelom, the right epicardium and other inferred aspects have been omitted. (After Jefferies, 1975, fig. 4, q.v. for greater detail.)

out is that this monstrous mitrate child must immediately have had its branchial openings on the opposite side of the theca to those of its parents.

All such problems are removed if the traditional and previously accepted view of the relationship between the faces of carpoids is followed. This is the interpretation indicated by the objective morphology of the fossils and so it is the interpretation advocated here. However, it demolishes in its entirety the calcichordate theory.

It appears that one of the issues that has influenced Jefferies greatly in his interpretation is the inferred life position of these animals which he discusses at length. Thus *Cothurnocystis* is interpreted as resting on the sea-floor with its cothurnoporoid surface upwards. *Mitrocystites*, on the other hand, rested with its paripores and more strongly plated surface upwards. These surfaces are regarded as homologous by Jefferies but, of course, this need not have anything to do with the fundamental morphology of the animals. As is indicated in Section V it seems likely that cornutes rested on their right side and mitrates on their left side, representing, perhaps, a change from suspension feeders to deposit feeders.

(2) The gill openings of mitrates

If further evidence is needed, what is finally fatal to the calcichordate theory derives from a problem that always has surrounded the mitrates. The later ones, especially the anomalocystitids, lack any thecal pores or orifices at all except for a thin anterior

slit. This leads to considerable problems in any conjectured reconstruction of the animal. Bather (1930), for example, complained of *Placocystites* that it "has puzzled me for more than forty years".

The calcichordate theory, based as it is largely on soft parts, demands very little of the mitrate skeleton. Its only real requirement is a pair of gill openings on the underside of the theca towards its posterior margins. In *Mitrocystella incipiens miloni* "paired, external branchial openings seem to have existed..." which are interpreted as forming along sutures which opened up (Jefferies, 1968*b*, p. 282). In *Mitrocystites mitra* (*op. cit.* p. 314) they are said to be situated in a similar position for "the break of slope...is not explicable if the plates...were merely sutured together". In forms with a somewhat flexible theca this provides at least a possible, albeit unlikely, interpretation. In the anomalocystitids, with their rigid theca, the situation is different. Jefferies & Lewis (1978) in their lengthy article describing *Placocystites forbesianus* and its relationships, discuss the gill openings of the theca twice. They write (p. 220): "There was a wide mouth anteriorly and there is evidence of right and left gill openings posteriorly. The ventral shield was presumably slightly flexible near the gill openings to allow them to gape." They continue (p. 226): "The branchial openings, by comparison with other mitrates, would be situated between M_{2R} and M_{1RV} on the right side, and M_{2L} and M_{1LV} on the left. Judging by the positions of the nerves inside the head, the left branchial opening may have been about twice as long as the right one...Also the rectum opened into the left atrium, not into the right one, so that faeces would have to leave the head through the left gill opening."

The theca of anomalocystitids is rigid. There are simply no openings that could be construed as gill openings in the theca of *Placocystites* (or any anomalocystitid for that matter). It would have been fatal indeed for these carroids to have followed the evolutionary course suggested by the calcichordate hypothesis.

It is concluded that the calcichordate theory is based on a number of initial propositions or interpretations which individually and collectively are highly unlikely, if not impossible. It leads to simple morphological requirements for which there is no evidence at all in the fossils themselves. Although the theory is here rejected, it should be noted that aspects of recent discussions can be maintained outside the context of the theory (e.g. the discussion of the ancestral vertebrate by Jefferies & Lewis (1978), p. 295 *et seq.*).

IV. THE ORGANIZATION OF CARPOIDS

Rejecting both the aulacophore and calcichordate theories, we come full circle in the interpretation of the organization of carroids. What follows is a fairly traditional and deliberately simplistic view.

Anomalocystitids such as *Placocystites* have as their only thecal opening a narrow distal slit, which clearly must have provided all intake and excretion by the animal. We are thus led to Gislén's (1930) discussion of carroid organization. Gislén had the vent serving a single intestinal opening, i.e. acting as both mouth and anus (as in brittle stars) with the cothurnopores of cornutes developed as drainage organs to

release excess water from the intestine during anal feeding. This interpretation is difficult to apply to mitrates, which lack the requisite pore. Although Bather (1913), and Ubaghs (1968*b*) have interpreted the major thecal opening of cornutes as an anus, Spencer (1938) regarded it as the entrance to a vestibule which held both mouth and anus. This is the interpretation favoured here, and it is lent weight by the proximity of the mouth and anal openings in contemporaneous echinoderms such as the *Cincta* (Fig. 13), i.e. it is here inferred that carpoids possessed a U-shaped intestine, rather than a blind one. Ubaghs (1968*b*) judges the integument surrounding this main orifice as highly flexible and suggested that an anus "could have been protruded". There would be more purpose in the animal protruding a mouth surrounded by tentacles.

There is no evidence of the presence of a water vascular system and associated subvective system in any carpoid. Certain pores have been interpreted as hydropores (e.g. Jefferies, 1969, p. 499, fig. 2) but they are evanescent in their occurrence and remain uncertain in their identification (Ubaghs, 1968*b*, pp. S523–525, gives a full discussion).

Particular attention is directed to the accessory pores of *Mitrocystites* – the so-called lateripores and paripores. Again there has been much difference in past interpretations. Bather (1926, 1929) envisaged them as entering the digestive system. Gislén (1930) saw them as branchial slits. Chauvel (1941) did not homologize them with the cornute thecal openings, and developed the thesis that the lateripores were goniopores and the paripores were hydropores. For Jefferies (1967 *et seq.*) they represent "transpharyngeal" and "cispharyngeal" eyes. As these openings connect with canals inside the theca which are interpreted as nerve canals they are here viewed as housing some form of external sensory organs, perhaps even light-sensitive ones.

The stele was obviously a strongly muscular organ, with a capacity to enroll, and was probably involved in both support and locomotion. It is likely that the proximal stele contained a cylinder of muscles with separate functions. Some could have attached the styloid-stylocone to the base of the theca with others connecting the imbricating plates of the proximal stele. The lumen of the distal stele could also have contained longitudinal muscles as well as those connected to the small imbricating plates which were interpreted by Ubaghs as cover plates. Thus the central longitudinal groove could have housed something similar to the peduncular nerve and haemal strand of the crinoid column and the lateral depressions could have served for insertion of transverse muscles which must have existed. Presumably there was a ganglion comparable with the aboral nerve centre of crinoids at the base of the theca.

The remarkable and persistent bilateral symmetry of the stele indicates that it was highly flexuous. The proximal stele consists of imbricating rings of basically four pieces of equal size in mitrates, and here a parallel is seen with the solutan stele (Caster, 1968, p. S593, notes that this is fundamentally tetraserial while the distal stele is biserial). It is reasonable to conclude that the solutan stele is homologous with the cornute and mitrate one.

The distinctive features of the carpoid stele were already developed in the earliest Middle Cambrian carpoids. Contemporary crinozoans have a stem weakly differentiated from the theca. Progressively, a typical pelmatozoan column evolved in such

forms in the early Palaeozoic. Although Jefferies (1967) originally homologized the crinoid stem and carpoid stele, he subsequently (1975) has viewed them as parallel developments. Such an interpretation is advocated here.

V. THE BIONOMICS OF CARPOIDS

Carpoids are usually found fossilized in silty or calcareous sediments in reasonable numbers, often giving the impression of having been engulfed and killed by an influx of sediment. Generally, they seem to have lived in a quiet environment, out of range of wave action. However, genera such as *Enopleura* are found as dissociated plates in calcarenites, perhaps indicating that some forms were adapted to a more turbulent environment.

As usual, there has been much difference of opinion as to the mode of life of these creatures. All authorities agree, however, that cornutes rested on the sea floor with the cothurnoporoid (ventral) surface upwards. Gislén (1930) believed that it swam or sculled forwards "through rapid contractions in lateral directions of the proximal part of the stem". Jefferies (1967, p. 173) envisaged *Cothurnocystis* as creeping backwards over the sea bottom, although the mechanics of this motion are not particularly clear. He writes: "The distal posterior stem would stick into the bottom by relaxing its muscles. The anterior stem would flex to one side, pulling the theca backwards. The distal portion of the stem would then lift itself off the bottom...." It is doubtful whether the distal stele could have been so manipulated and, if it could, whether any motion of the theca could have resulted (unless the distal stele were deeply buried for its entire length).

The marked asymmetry of the theca of cornutes such as *Cothurnocystis* would suggest little motility. In particular it is difficult to envisage forms with well-developed marginal spines (such as *Chauvelicystis*) as motile (Fig. 9). Perhaps such forms could move by first raising the anterior end of the theca slightly above the sea floor and then producing lateral movements of the proximal stele, i.e. the animal would move forwards by wriggling the stele from side to side.

The highly muscular and flexible stele is here seen as the means by which the animal obtained sufficient purchase on the soft sea-floor to raise the theca above the sea-floor to permit filter-feeding in the gentle bottom currents. Its flexuous nature would have been invaluable should the animal have been engulfed by sediment or turned upside-down by other chance events.

In mitrates the theca is far more bilaterally symmetrical, suggesting a much more motile mode of life. The slit-like opening to the theca is located at the anterior end and seems adapted for shovelling up sediment. It seems likely that these animals were deposit feeders. Again there are widely disparate views as to their mode of life. Jefferies (1973, 1975) in general holds that mitrates crawled backwards either over or through a muddy sea floor; he infers that they could swim, e.g. "*Lagynocystis* rotated as it swam in the same manner and direction as larval amphioxus" (Jefferies, 1975, p. 314). Extensive accounts of the rearward mode of locomotion of carpoids are provided by Jefferies & Prokop (1972, pp. 91-104) and Jefferies & Lewis (1978,

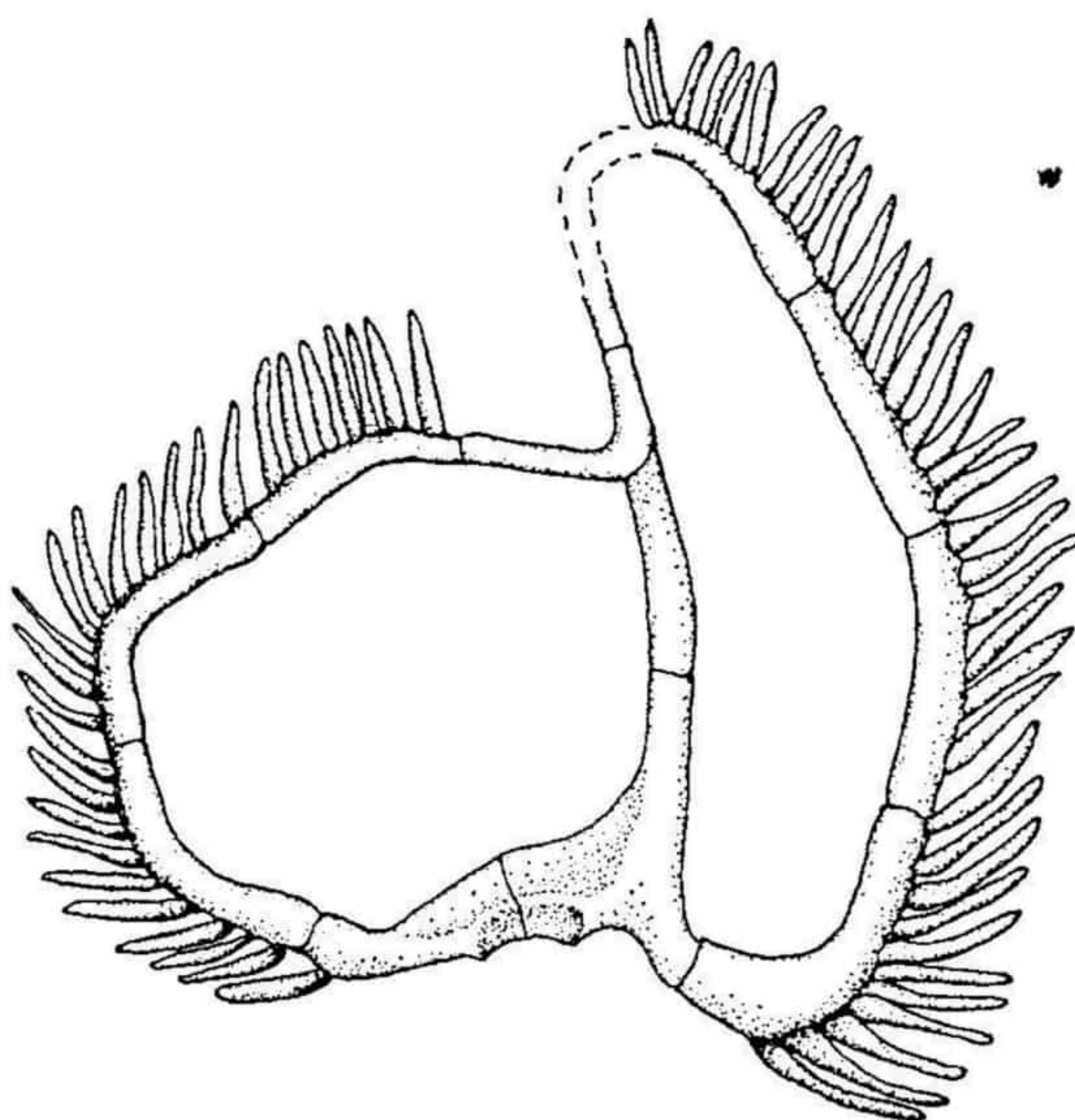


Fig. 9. Spines and marginal frame of the cornute *Chauvelicystis spinosa* Ubaghs.
(After Ubaghs, 1970, fig. 23.)

pp. 232–239). Their interpretation of *Mitrocystites* is depicted in Fig. 10. The distal surfaces of the dorsal ossicles are described as “bearing surfaces”. cursory examination of the figure reveals the impossibility of such an interpretation unless the whole stele was protrudable (which, patently, it was not). If *Mitrocystites* moved backwards in the fashion envisaged by these authors, then clearly the smaller inner stele plates would constitute the “bearing surfaces”.

Much emphasis is placed by Jefferies & Lewis (1978) on the morphology of the sinuous transverse cuesta-like ribs, seen for example in *Placocystites*, in determining the direction in which the animals moved. Such low ridges have their steeper sides facing anteriorly and by comparison with the burrowing bivalve *Divaricella* and the mole crab *Emerita*, the ridges are interpreted as adaptations for gripping the sediment during movement. Such a comparison is here considered to be inappropriate. The echinoderm skeleton is an endoskeleton, not an exoskeleton, and is covered in life by an exodermal layer, the epidermis. To be sure, this covering may be rubbed off prominently projecting parts, such as the tips of spines. It is only in the spines of cidaroid echinoids (and some stirodonta) that dense ‘dead’ calcite forms the outer layer of the skeleton; hence the spines are often covered in encrusting organisms. The presence of an epidermis covering the theca of carpoids would have nullified any directional effect provided by the external ridges. This objection applies to similar arguments such as the imbrication of thecal plates (Jefferies, 1968*b*, p. 310). A most elaborate interpretation has been given of the mode of life of *Placocystites* in which the animal is envisaged as ploughing backwards through the upper layers of the muddy sea-floor, with the oral spines developed to remove mud from around the mouth as it fell off the anterior margin of the theca, the lateral sweeps of the spines

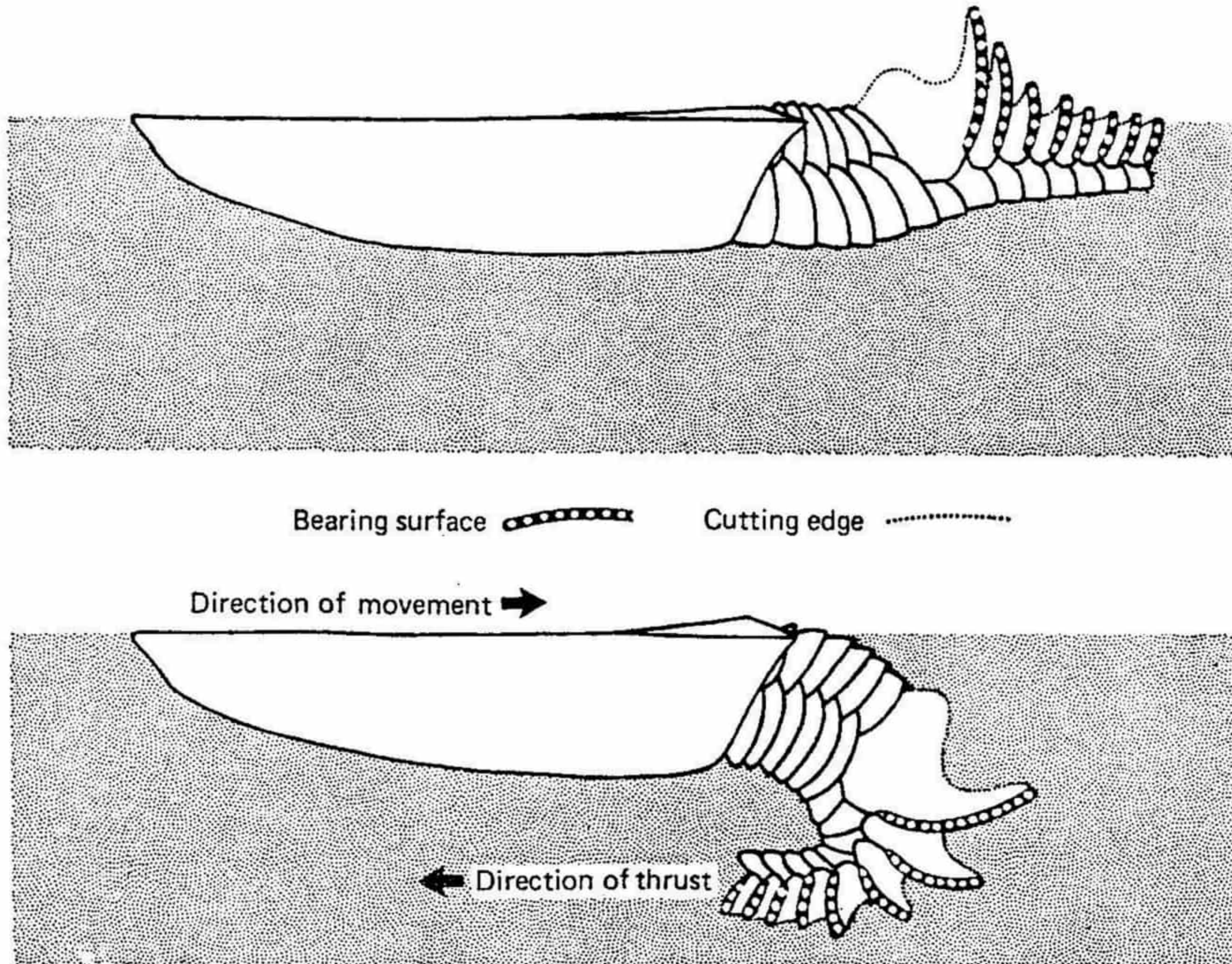


Fig. 10. Mode of backward locomotion of *Mitrocystites* suggested by Jefferies & Prokop (1972).
(After Jefferies & Prokop, 1972, fig. 11.)

being synchronized with the action of a strong velar pump (Jefferies & Lewis, 1978, pp. 237-238).

One must agree with Jefferies that mitrate carpoids were adapted for life on or slightly buried in bottom muds, that they were deposit feeders, and that the stele was adapted for locomotion. However, I believe they are best interpreted as moving forward.

In this interpretation the mitrate would slowly bring its stele through the sediment until it was arched beneath the theca and then would straighten it suddenly. The flanges on the distal stele plates and of the stylocone in particular (which are otherwise inexplicable) therefore constitute the bearing surfaces pushing against the sediment to give the forward movement. The oral spines of anomalocystitids might have been used to stabilize this motion and also to funnel the food-rich surface layers toward the mouth. Perhaps the animals moved hardly at all and then only when feeding.

VI. THE PHYLOGENETIC POSITION OF CARPOIDS

As indicated above, the comparison of carpoids is with their contemporary echinoderms, and, with the interpretation presented here, some review of their phylogenetic position is required. Although knowledge of ancient fossil echinoderms has increased greatly over the last decade (Ubaghs, 1971, 1975; Paul, 1977; Durham, 1978) there has been no corresponding increase in the understanding of the phylogenetic relationships of the different groups. A review of the development of concepts is timely.

Bather (1899, 1900) proposed that the most obvious characters of echinoderms (such as radial symmetry and the ambulacra) were produced by their passage through an attached or 'pelmatozoic' stage in evolution. The organisms became attached by the pre-oral part of the body which became elongated into a peduncle, the principal organs underwent torsion, bringing the mouth to the upper surface (as seen in the development of living crinoids). After attachment and torsion, radiating extensions of the food-gathering system developed around the mouth. Bather depicted these conjectural phylogenetic changes by elaborating Semon's (1888) archetypal echinoderm – his dipleurula animal – and sought examples from the fossil record depicting this order of change. Although Bather originally regarded carpoids as stemmed echinoderms, he later (1929, 1930) regarded them as an independent branch of the phylum, lacking radiate symmetry – "echinoderms that never traversed the evolutionary roads of the other classes".

In recent years such concepts have fallen from favour. Hyman (1955), for example, concluded that they failed to explain the water vascular system with its coelomic origin and the degeneration of the organs of the right side of the body. So dipleurula has been relegated to the concept of the ancestral larval form of the phylum.

Despite statements to the contrary, there is some reasonable support for Bather's concepts from the fossil record. Both Bather and Heider (1922) inferred that the pentamerous condition of echinoderms arose after fixation and torsion and was also preceded by a tri-radiate arrangement. Three ciliated grooves with tentacles spread out on the theca diverging from the mouth, one in a direction opposite the anus (a posterior groove being so prevented) and one on each side. The two lateral grooves then each divided, presumably as a response to more efficient food gathering. Bather used as an example of this process a morphological series involving some Ordovician cystoids which, at the time, were viewed as among the oldest and most primitive of echinoderms. This proposition has recently been restated by Fell (1966).

Ubaghs (1968a, p. S49) presents a strongly critical view of all this. He writes: "A triradiate condition of the subventral system observed in a very small number of fossil echinoderms, represents a secondary character, without doubt...the cystoids to which Bather referred comprise a strongly specialized group preceded in time by other classes...The edrioasteroids exhibit a well defined pentamerism from their first appearance in the lower Cambrian and the eocrinoids possess multiple brachioles generally distributed in five groups...."

A wide variety of different types of echinoderm are now known from the Lower and Middle Cambrian (Ubaghs, 1975), although their sporadic occurrence indicates that their order of appearance is no real measure of evolutionary relationships. Apart from isolated eocrinid (?) plates which occur close to the base of the Cambrian in eastern California, the first records of the phylum are of middle Early Cambrian age, when helicoplacoids, eocrinoids and edrioasteroids occur (Sprinkle, 1976; Durham, 1978). By the Middle Cambrian cornute and cinctate carpoids, ctenocystoids and cyclocystoids had appeared. Of particular note is the occurrence of the first branchiate echinoderm *Echmatocrinus* in the Middle Cambrian Burgess Shale. Other groups,

such as the cycloids, cyamoids, camptostromatoids, had appeared by then but their organization remains poorly understood.

These early echinoderms can be divided into two groups. Firstly there are those which were attached and had undergone torsion, bringing the mouth and anus to the upper surface of the theca (edrioasteroids, eocrinoids, *Echmatocrinus* and probably the cyclocystoids). The others lack radial symmetry and appear to have been unattached.

The denial by Ubaghs of the primitive triradiate character of the ambulacra of edrioasteroids and eocrinoids cannot be supported. Bather (1898, 1914, 1915) and Foerste (1914) have discussed the fundamentally triradiate nature of edrioasteroids, as seen in the midlines of the oral area, the structure of the oral frame and as emphasized by the ontogeny of different species (Fig. 11). Bell (1976*a*, p. 35) in his recent revision of the class, states: "Evidence of a basic triradiate symmetry suggests that the pentaradial pattern is secondary superposition on an earlier triradiate pattern", and this conclusion is further emphasized by him elsewhere (Bell, 1976*b*). If the soft bodied late Precambrian fossil *Tribrachidium* is viewed as an echinoderm (Glaessner & Wade, 1966; Nichols, 1967) and a precursor to the edrioasteroids then this triradiate character is even more marked. In eocrinoids the situation is less obvious. Even so, Sprinkle (1973, p. 42) has noted that "The unequal development of five ambulacra in some early eocrinoids suggests that the observed pentameral symmetry may be derived from an older triradiate arrangement of ambulacra." Very little can be said of the symmetry of *Echmatocrinus*, as even the number of brachia is uncertain.

Stephenson (1979) has attempted to explain the triradiate pattern of ambulacra as an adaptive simplification of a fivefold plan, and so rejects the concept of a trimerous stage in echinoderm evolution as unnecessary. This viewpoint is not supported by the fact that it is the oldest of echinoderms with ambulacra that best show a triradiate pattern.

It is also noteworthy that the first eocrinoids (and *Echmatocrinus*) possess a peduncle weakly differentiated from the theca, and there exists a clear morphological series among eocrinoids to produce a stem with columnals in the Middle Cambrian (Fig. 11) whereas in crinoids this did not take place until the latest Cambrian-earliest Ordovician (Sprinkle, 1973, pp. 38-39), along the lines suggested by Bather (1900, p. 48, p. 105) for the origin of the crinoid column. The fossil record clearly indicates that the carpoid stele is independent from the crinoid column and that the structures cannot be regarded as homologous (cf. Eaton, 1970; Jefferies, 1975).

Bearing in mind the above discussion we may present the following speculative phylogeny of early echinoderms. With Grobben (1924), Jefferies (1969) and Eaton (1970) we envisage a pterobranch-like echinoderm ancestor organized something after the style of *Cephalodiscus* (Fig. 12). There are good reasons for invoking such an ancestor because the early larval stages of echinoderms offer striking similarities with the tornaria larva of enteropneustids – in the circumoral ciliated band, the apical sensory plate, the shape and subdivision of the digestive tract, the division of the coelom and so on. Moreover, the ambulacral system of echinoderms is to be compared with the pterobranch lophophore since both are derived from the middle coelom and both have the form of coelomic evaginations.

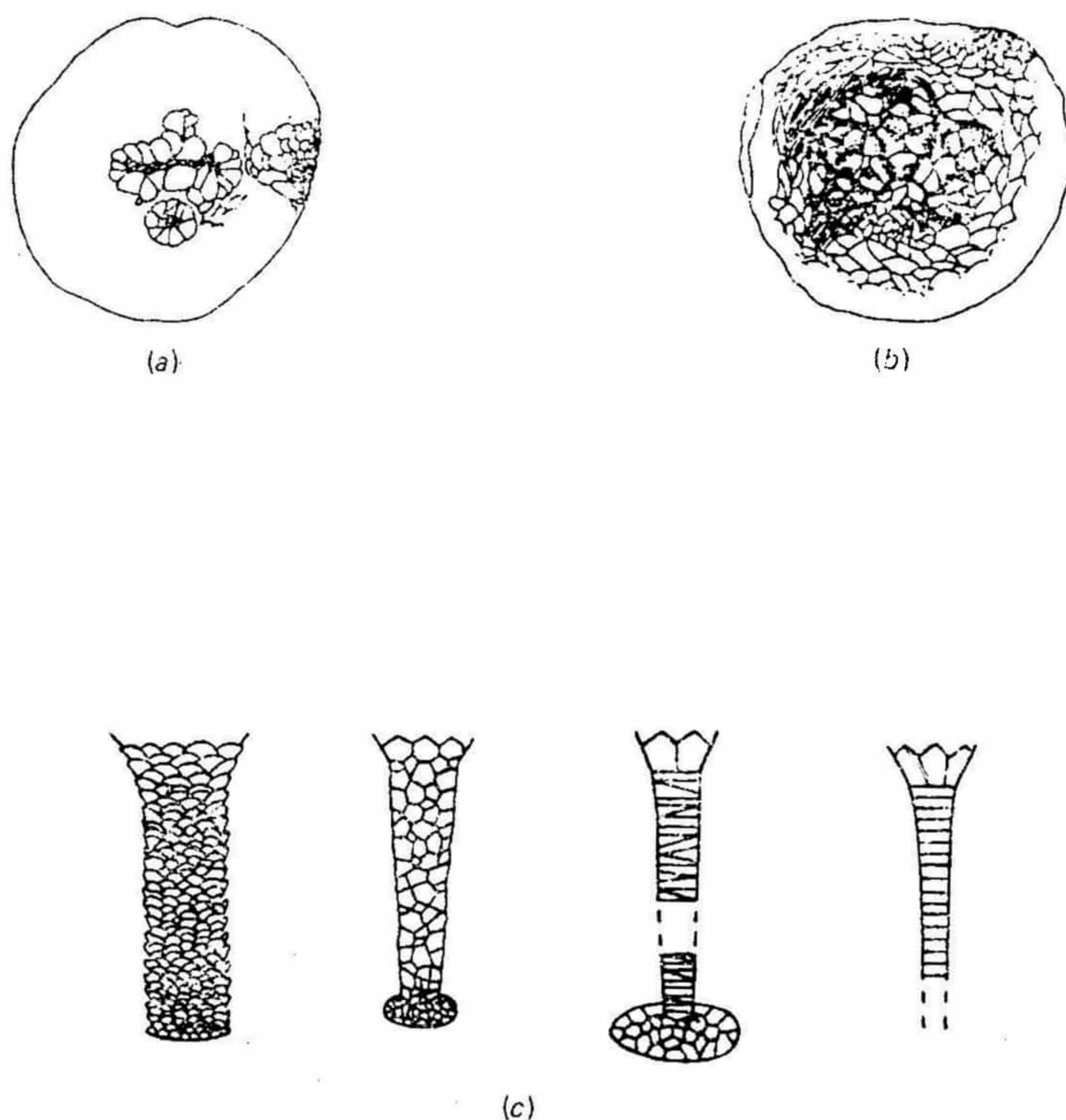


Fig. 11. (a, b) Small specimens of the edrioasteroid *Belochthus orthokolus* showing the basically triradiate symmetry of the ambulacra. (After Bell, 1976, fig. 8) (c) Morphological series of Middle Cambrian eocrinids showing the development of a columnal-bearing stem from a peduncle weakly differentiated from the theca. (After Sprinkle, 1973, fig. 14.)

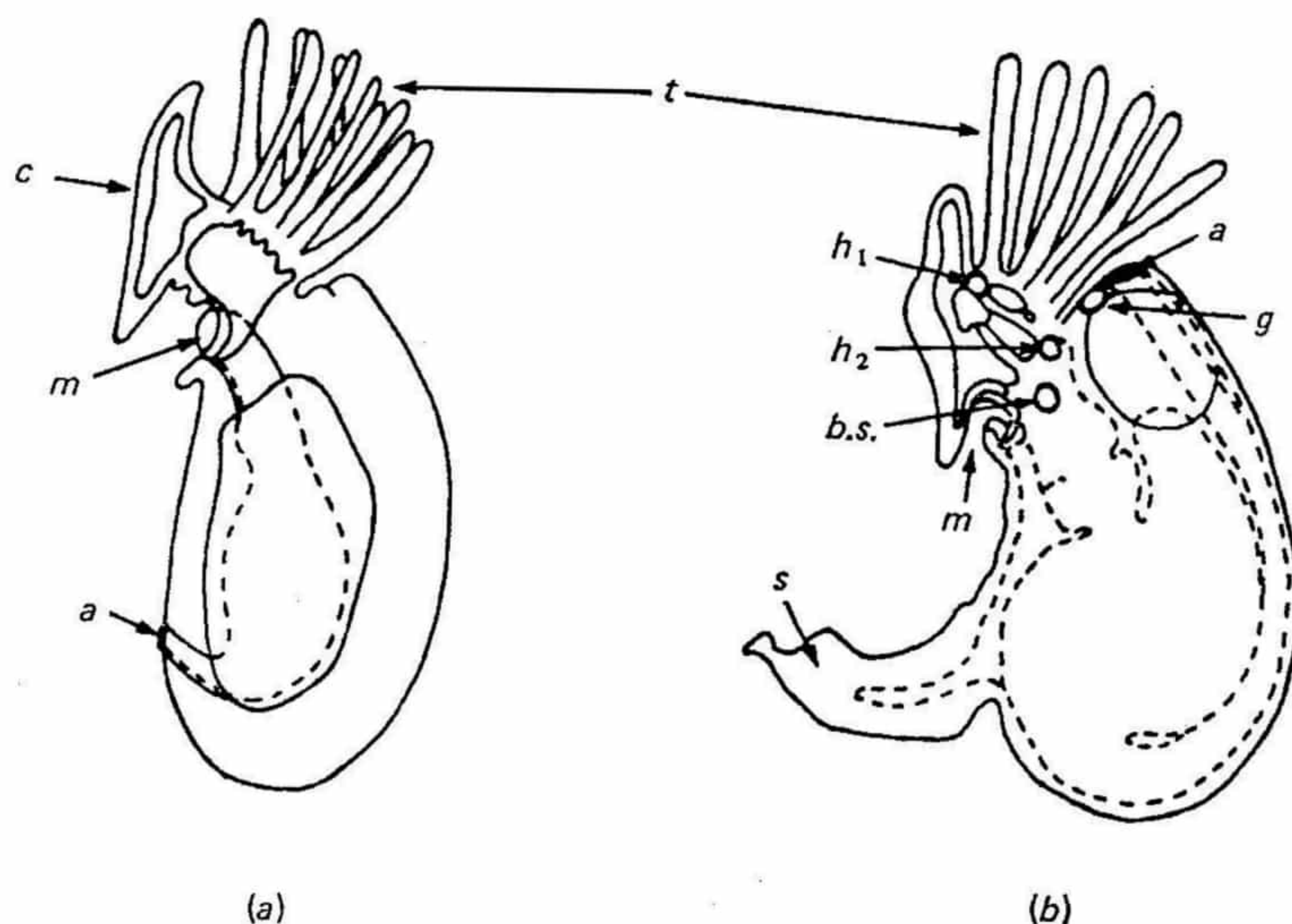


Fig. 12. (a) Theoretical *Cephalodiscus*-like echinoderm ancestor proposed by Grobden. (After Ubaghs, 1968a, fig. 20.) (b) *Cephalodiscus*. (After Jefferies, 1969, fig. 18.) a, anus; c, cephalic shield; bs, brachial slit; g, gonopore; h₁, procoel pore; h₂, mesocoel pore; m, mouth; s, stem with peduncular nerve; t, tentacles.

It can be speculated that animals of this type became motile and took to moving over the sea-floor, lying on the right side. Thus were lost the openings of the right side of the body, the right proto-coel pore, the right mesocoel pore, the right gonopore and the right tentacles. The left proto-coel and mesocoel fused to give the hydropore and the calcite endoskeleton began to develop. Thus evolved an essentially free-moving asymmetrical animal in which the tentacles surrounded the mouth and the hydropore and gonopore were retained in proximity to the mouth. The U-shaped digestive tract was retained in forms such as *Gyrocystites* and also in the cornutes but in others, such as the ctenocystids and the solutan carpoids, it became straight. These organisms became more nearly bilaterally symmetrical in response to a more motile mode of life and this is seen in the ctenocystoids and also the mitrate carpoids. The mitrate carpoids became adapted as deposit feeders, resting on the opposite side of the theca from their ancestral cornutes. Mostly the unattached echinoderms did not require skeletal support for the tentacular system which thus was not highly developed and was merely represented by a circle of tentacles around the mouth. However, one group, the solutan carpoids, developed a single food gathering arm or brachiole. The unattached, originally asymmetric branch of the phylum became extinct by the Devonian.

The other group (the crinozoans and edrioasteroids) became attached and underwent torsion, bringing the mouth and anus close together on the upper surface of the theca. Food grooves (firstly on a threefold plan) developed and these ultimately became pentamerally arranged; the pelmatozoan column also developed. Because of their attachment, the animals of this group had need for a greatly extended podial system and so the water vascular system became associated closely with the skeleton and developed much more fully. This group gave rise to all the later echinoderms.

It will be noted that the above statement of the phylogeny of early echinoderms, summarized in Fig. 13, is similar in broad principle to the views of Bather (1900, 1929) and, indeed, parallels in part the recent statement of Ubaghs (1975).

VII. SUMMARY

1. Carpoids are interpreted as early echinoderms representing a stage of evolution before attachment and the development of pentameral symmetry.

2. The interpretation that the carpoid stele is a feeding arm or aulacophore is rejected largely because:

- (a) It is difficult to envisage a food groove passing through the envelope of muscles in the proximal stele; in some carpoids (e.g. *Lagynocystis*) a curtain of calcite separates the theca from the proximal stele.
- (b) It is doubtful if the so-called cover plates could open in later mitrates.
- (c) The cornute stele is to be compared with the solutan stele which is not subvective in nature.

3. The stele is therefore interpreted as an analogue of the pelmatozoan stem. Cambrian crinozoans show progressive differentiation of the peduncle or stem, indicating that the stele is not an homologous structure.

4. The calcichordate theory, which holds that mitrate carpoids were ancestral to acraniates, tunicates and vertebrates is also rejected for the following reasons:

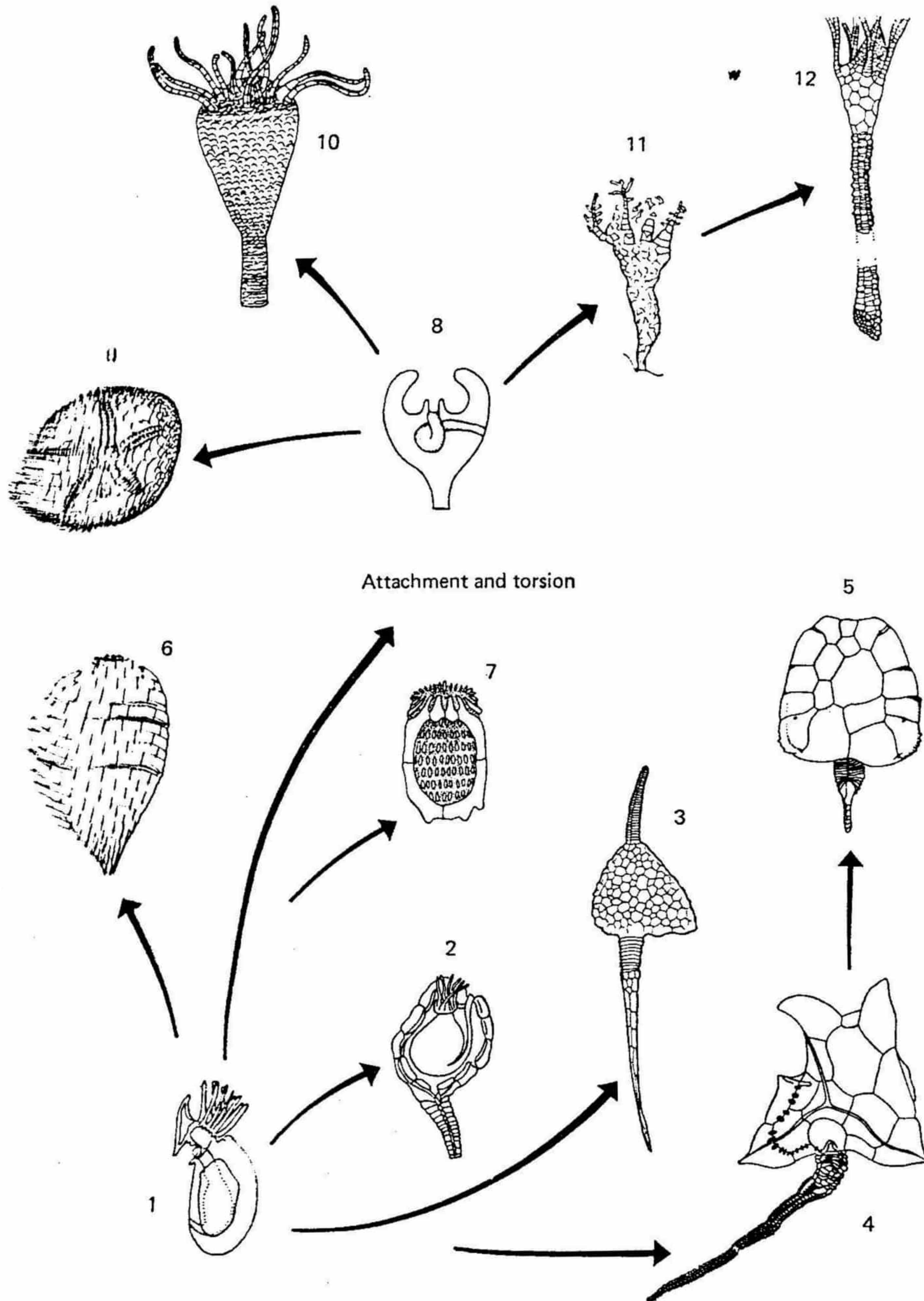


Fig. 1. Suggested phylogenetic relationships of primitive echinoderm groups. 1, Hypo-phylodiscus-like echinoderm ancestor; 2, *Gyrocyttis* – a cinctate carpoid. 3, *Solutes*. 4, *Coronata*. 5, *Mitrates*. 6, *Helicoplacoids*. 7, *Ctenocystoids*. 8, Crinoid-like form in which attachment and torsion has taken place. 9, *Edrioasteroids*. 10, *Eocrinoids*. 11, *Echmato-branchiate* echinoderm. 12, True crinoids.

- (a) Identification of the various thecal pores of cornutes demanded by the theory is highly contentious. This applies not only to the so-called gill slits, but also the mouth and anus. In particular the interpreted rectum passes through solid calcite skeleton in certain cornutes.
- (b) Interpretation of the stele as a notochord is conceptually difficult. It is impossible to see how such a structure could have functioned, enclosed as it was in calcite plates, or why it would have been necessary.
- (c) The vertebrate-like brain is based on major reconstruction. There would have been no room for such an enlarged ganglion among the stele muscles at the base of the theca.
- (d) The theory demands loss of calcite skeleton in three independent lines of descent. Again it is difficult to see how this could have been brought about. Indeed the evolution of carpoids shows the progressive development of a more rigid and box-like theca.
- (e) The fossil record suggests that Ordovician mitrates could not have given rise to late Cambrian vertebrates and middle Cambrian acranians.
- (f) The homology of the stele in cornutes and mitrates indicates that the thecal faces are to be identified in some other way than that required by the theory. This leads to a complete break-down in the proposed homology of the internal thecal chambers of cornutes and mitrates.
- (g) The calcichordate theory requires there to be two posterior gill openings under the theca of mitrates. Such openings do not exist in later mitrates such as the anomalocystitids.

5. The cothurnopores of cornute carpoids are to be compared with the respiratory modifications of contemporary Palaeozoic echinoderms (epispires, diplopores, goniospires). They may have been a response to low oxygen concentration in sea water at the beginning of the Palaeozoic.

6. Cornute and mitrate carpoids probably possessed a U-shaped gut, similar to the *Cincta*, rather than a blind one. Along with this group and the ctenocystoids they possessed a tentacular system around the mouth which did not become involved in the endoskeleton.

7. Cornutes are interpreted as being hardly motile, using their stele to raise the theca above the sea floor. In all probability they were filter-feeders.

8. Mitrates, in contrast, were deposit feeders that moved forward through the upper layers of the muddy sea-floor.

9. Early echinoderms known from the fossil record can be divided into two groups. There are attached ones which had undergone torsion, bringing the mouth and anus together on the upper surface of the theca. This group developed pentameral symmetry. The second group, to which belong the carpoids (cornutes, mitrates, solutans and cinctates) and the ctenocystoids, was unattached and its representatives lack all trace of pentameral symmetry.

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X. ADDENDUM

Throughout this review the orientation of anomalocystitids is that advocated by Jefferies & Lewis (1978); i.e. the flat face of the theca is taken as the dorsal or superior surface and the convex face as the inferior one. Analysis of the morphology of a new Australian anomalocystitid discussed elsewhere suggests that a return to the traditional and opposite orientation of mitrates is warranted. Such a change in interpretation does not affect the validity of the main arguments presented above; it means, however, that cornutes and mitrates rested with the same side of the theca on the sea-floor. The discussion given in Section V and VI should be so modified.